AN ABSTRACT OF THE THESIS OF

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Riparian plant detritus is a major source of organic matter for many headwater stream ecosystems. However, relatively little is known about organic matter dynamics in stream reaches flowing through non-forest riparian zones. In addition, the role of seasonal flooding in detrital recruitment and retention in headwater streams is poorly understood.

We examined spatial and temporal patterns of coarse particulate organic matter (CPOM) and associated carbon and nitrogen inputs, transport, retention, and storage along longitudinal gradients from coniferous forest reaches to downstream floodplain meadow reaches in two second-order tributaries of the Upper Grande Ronde River in Oregon. CPOM inputs to the forest reaches (187- 210 $g \cdot m^{-2} \cdot yr^{-1}$) were dominated by litterfall and lateral movement of woody material, needles, and alder leaves. In contrast, annual CPOM inputs to the meadow reaches (214 - 267 $g \cdot m^{-2} \cdot yr^{-1}$) consisted primarily of herbaceous material entrained by the stream during spring high-flows. On a stream length basis, annual CPOM loading was estimated to be higher in the meadows than in the forests. The concentration and daily transport of CPOM was highest during spring

high-flow and lowest during summer base-flow. Also, the concentration of CPOM was significantly higher in the forest reaches during high flow than in downstream reaches. Large wood, small wood, and coarse benthic organic matter (CBOM) was significantly higher in the forest reaches than in downstream meadow reaches. In addition, CBOM was strongly associated with large wood abundance among all reaches.

CPOM retention was estimated by releasing tracer leaves into both streams during base-flow and high-flow and calculating retention as the removal rate of introduced leaves from transport using a negative exponential decay model. Average travel distances of leaves ranged from 0.9 to 97m over all reaches. During high-flow, the forest reaches were significantly more retentive of CPOM than meadow reaches. However, in the meadows, there was much more retention on the floodplain. Despite large variation among reaches, thalweg depth and stream width explained the most variation in retention rates among all reaches.

Our results emphasize the importance of spatial heterogeneity in hydro-geomorphic characteristics and riparian plant composition to our understanding of the structure and function of headwater stream ecosystems. If our conceptual frameworks of energy and material flow in stream and riparian ecology are to become more general in their applicability, research must explicitly address reach and valley-segment scale patchiness in structure and processes within the headwaters. Moreover, management strategies must recognize that spatial and temporal heterogeneity in stream and riparian ecosystems is biologically meaningful. Better understanding and management of these ecosystems is essential to maintaining and restoring biodiversity.

Forests to Floodplain Meadows: Detrital Dynamics in Two Headwater Streams

by

E.N. Jack Brookshire

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E.N. Jack Brookshire

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INTRODUCTION

One of the most general patterns underlying variability across ecosystems is the universal requirement of all organisms for energy and matter. General patterns among ecosystems result from the constraints of the abiotic and biotic environment and the tradeoffs that organisms experience with these constraints (Tilman 1989). The most basic of these environmental constraints are the laws of thermodynamics and the availability of nutrients that are limiting to growth (Schlesinger 1997). The approach of ecosystem ecology has been to identify system boundaries, assemble models of components and flow, measure material and energy pools and their rates of flux between components, and to determine the processes controlling the fluxes (Pickett et al. 1994).

The earliest ecological studies of energy and material flow were conducted in aquatic ecosystems. The pioneering studies of Odum (1957) and Teal (1957) in spring ecosystems were the first attempts to quantify the relative contributions of organic matter from different sources. Among others, they concluded that energy was derived from two major sources, allochthonous material from the adjacent terrestrial environment and autochthonous material produced by aquatic autotrophs. Ecologists next applied the organic matter budget approach to small woodland streams. Fisher and Likens (1973), in their classic study of Bear Brook, estimated that over 99% of the energy input into the stream was allochthonous material derived from the adjacent riparian zone. This study was followed by numerous studies demonstrating a general dominance of allochthonous

(Minshall 1988). It has followed that a central premise of stream ecology for more than two decades has been the importance of terrestrial-aquatic linkages to the dynamics of stream ecosystems (Cummins 1974, Hynes 1975, Gregory et. 1991, Wallace et al. 1997).

Riparian areas are defined as three-dimensional zones of abiotic and biotic interaction between terrestrial and aquatic ecosystems (Gregory et al. 1991). Riparian areas have become increasingly recognized as complex and diverse ecosystems critical to the survival of aquatic and terrestrial biota and essential in maintaining water quality and landscape-level biodiversity (Gregory et al. 1991, National Research Council 1992, Naiman et al. 1993). One important function of riparian areas is the supply of allochthonous coarse particulate organic matter (CPOM = organic matter > 1mm) to stream food webs (Cummins 1974, Wallace et al. 1997). Indeed, a large body of research exists on the inputs, outputs, and storage of riparian CPOM in stream ecosystems, most of which has been conducted in forested headwater streams (Minshall 1988, Webster and Meyer 1997).

A critical contribution to stream and riparian ecology has been the recognition that interactions among landforms, geomorphic processes, and organisms shape ecosystem patterns and processes over various temporal and spatial scales (Vannote et al. 1980, Swanson et al. 1988). Landform features and associated disturbance regimes strongly influence the distribution, composition, and structure of riparian zones and energy and nutrient flow within them (Swanson et al. 1988, Gregory et al. 1991, Montgomery 1999). As a consequence, patchiness in riparian vegetation can influence the quantity and quality of allochthonous detritus (Pringle et al. 1988, Johnson and Covich 1997). The chemical quality of detritus is a major determinant of availability to aquatic biota (Webster and

Benfield 1986). However, because of the flowing nature of streams, detritus must be physically retained before it is available to most microbial and animal consumption (Lamberti and Gregory 1996). Stream reaches differ greatly in their capacity to retain and store detritus, depending upon channel morphology, the abundance of large wood and other retentive features, and flow conditions (Speaker et al. 1984).

Just as different valley segments and stream reaches are shaped by particular geomorphic processes (Montgomery 1999), it is likely that the dominant processes by which allochthonous organic matter is exchanged between streams and adjacent riparian zones vary greatly in magnitude and temporal and spatial dynamics among different reach types. Most stream organic matter studies have focused on litterfall inputs, processing, and transport in forested headwater streams (Webster and Meyer 1997) or differences among sites in the relative contributions of allochthonous versus autochthonous energy sources (Minshall 1978, Bilby and Bisson 1992).

Very few studies have quantified inputs and movement of riparian detritus in stream reaches bordered by natural non-forested riparian zones such as tundra, meadows, and grasslands (Peterson et al. 1986, Gurtz et al. 1988, Scarsbrook and Townsend 1994). In addition, though the importance of seasonal flooding to organic export has been recognized for some time (Fisher and Likens 1973), detrital exchange between streams and floodplains, particularly herbaceous-dominated floodplains, is poorly understood. Indeed, the major conceptual model of headwater streams in lotic ecology is that of a linear, uniformly closed-canopy, first-order tributary with high levels of leaf inputs (Minshall et al. 1992, Fisher 1997). The lack of information on energy and nutrient flow in non-forested small streams and the influence of seasonal flooding on detrital import

hinders the development of more holistic conceptual frameworks in stream ecology. Moreover, our lack of understanding of such systems and processes impairs our ability to effectively manage and preserve riparian and stream ecosystems.

Riparian and stream ecosystems are currently being degraded and destroyed at the highest rate in history (National Research Council 1992). Causes of riparian and stream degradation are numerous but include logging, agricultural production, water diversion, road construction, channelization, urbanization, and livestock grazing. Riparian and stream ecosystems are considered two of the most endangered ecosystems types in the nation (National Research Council 1995) and are associated with a disproportionate number of rare and endangered species (Naiman et al. 1995). For example, in the Pacific Northwest, habitat degradation, including the destruction of riparian areas, is associated with >90% of the documented extinctions and declines in native salmonid populations (Nehlsen et al. 1991, Gregory and Bisson 1997).

In northeast Oregon, like in much of the western U.S., one of the most pervasive forms of riparian habitat degradation is livestock grazing (Kauffman et al. 1997). In particular, highly productive montane meadow riparian ecosystems have historically been used for livestock grazing. Among other things, livestock grazing can result in decreases in native plant species diversity and biomass, loss of animal habitat, increased stream water temperatures, bank erosion, and channel incision and widening (Kauffman and Krueger 1984, Bestcha et al. 1991, Fleischner 1994, National Research Council 1995, Kauffman et al. 1997). Due to the ubiquity of historical and current livestock grazing in the region, few examples of relatively unperturbed floodplain riparian meadows occur. Similarly, few examples of relatively undisturbed coniferous forest systems occur in the

region due to extensive logging (Case 1995). Despite the fact that several federally listed threatened and endangered salmon and steelhead stocks inhabit headwater tributaries in the region, livestock grazing in riparian zones is still common (Kauffman et al. 1997). It is likely that both livestock grazing and logging strongly influence the quantity and quality of allochthonous organic matter flow in headwater stream ecosystems. Information on the processes of detrital organic matter exchange in relatively undisturbed floodplain meadows and coniferous forests is required. This would provide base-line data on structure and function and may advance our ability to effectively manage these ecosystems.

In this thesis I summarize the results of my research on detrital organic matter dynamics in two headwater streams in northeast Oregon. The major objective of the study was to quantify and compare the inputs, chemical quality, transport, retention, and storage of allochthonous organic matter in relatively undisturbed upstream coniferous forest reaches and downstream floodplain meadow reaches of West Chicken Creek and Limber Jim Creek, two second order tributaries to the Upper Grande Ronde River. The thesis is divided into two chapters, the first of which (Chapter 2) describes CPOM inputs, associated carbon and nitrogen inputs and C:N ratios, transport, and storage in the two streams. In chapter three, I describe the results of a leaf release study designed to estimate physical CPOM retention during spring high-flow in both forest and meadow reaches and during summer base-flow along the longitudinal gradients from forest to meadow reaches in both streams.

CHAPTER 2

Influence of Riparian Vegetation and Seasonal Flooding on Organic Matter Dynamics in Two Headwater Streams

E.N. Jack Brookshire

CHAPTER 2

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ABSTRACT

In forested headwater streams, allochthonous detritus is a major source of energy and nutrients for aquatic organisms. However, headwater streams are generally not uniformly forested. Patterns of organic matter import and movement occurring over small longitudinal scales and between distinct riparian zones with contrasting hydro-geomorphic characteristics are poorly understood. We investigated coarse particulate organic matter (CPOM) inputs to coniferous forest and downstream floodplain meadow reaches of two second-order tributaries of the Upper Grande Ronde River in northeast Oregon. CPOM was analyzed for carbon and nitrogen concentrations to estimate quality and total particulate inputs of these elements. In addition, we measured the transport and storage of CPOM along the short longitudinal gradients from forest to meadow in both streams.

CPOM inputs to the forest reaches (187- 211 $g \cdot m^{-2} \cdot yr^{-1}$) were dominated by litterfall and lateral movement of woody material, needles, and alder leaves. Annual stream surface area inputs to the meadow reaches were similar (214 - 267 $g \cdot m^{-2} \cdot yr^{-1}$) but consisted of herbaceous material (primarily sedge) entrained by the stream during spring high-flows. C:N ratios of dominant inputs were higher in the forests (41-104) than in the meadows (21 - 57). Alder leaves accounted for 35 - 70% of particulate N inputs to the forests. On a stream length basis, annual CPOM loading was estimated to be higher

in the meadows (778 -1182 g · m^{-1} · yr^{-1}) than in the forests (392 -621 g · m^{-1} · yr^{-1}). During high-flow, CPOM concentrations were significantly higher in the forest reaches than in downstream reaches. Regressions between discharge and CPOM concentration (mg/l) were stronger in the forests than in the meadows. Large and small wood and coarse benthic organic matter (CBOM) were significantly higher in the forest reaches than in downstream meadow reaches. Moreover, CBOM was strongly associated with large wood abundance among all reaches. Our study suggests that reach-scale differences in CPOM quality and consequent decomposition rates, physical retention, and the relative influence of seasonal flooding can determine detrital dynamics in headwater streams.

INTRODUCTION

Riparian plant detritus strongly influences trophic structure, energy and nutrient dynamics, and physical complexity in small streams (Wallace et al. 1997, Meyer et. al 1988, Gregory et al. 1991). Because light attenuation by tree canopies often limits algal and macrophyte growth (Minshall 1978), carbon flow within many headwater streams occurs through detrital food webs (Fisher and Likens 1973, Cummins 1974). In both terrestrial and aquatic ecosystems, detritus is incorporated into food webs through rapid leaching of soluble material, fungal and bacterial breakdown, physical fragmentation, and invertebrate activity (Wagener et al. 1998, Webster and Benfield 1986, Anderson and Sedell 1979). In stream ecosystems an understanding of the fluvial transport of detritus is central to determining its role in system carbon dynamics. Complex channel morphology (Sedell et al. 1978) and the presence of large wood (Bilby and Likens 1980) in small

forested streams facilitate particulate capture and retention and thus reduce losses of coarse particulate organic matter (CPOM: material >1mm) downstream.

Because ecosystem processes in stream reaches are longitudinally linked to upstream processes and laterally linked to adjacent floodplains, understanding reach-scale CPOM dynamics in streams requires evaluation of terrestrial CPOM input, transport, retention, storage (Wallace et al.1995), and lateral exchange between streams and riparian zones during high-flow events (Cuffney 1988). Residence time of organic matter in streams is a function of physical trapping by in-stream structures and chemical quality, that influences decomposition rates. Interaction among these processes and with channel geomorphology, hydrological processes, and water column characteristics, ultimately determines the biotic availability of CPOM in stream ecosystems.

Within mountainous headwater drainages, spatial variability in landform features and associated geomorphic processes control the abundance and distribution of aquatic habitats over various temporal scales (Montgomery 1999). Landform features and disturbance processes may produce compositionally discrete patches of riparian vegetation (Swanson et al. 1988, Gregory et al.1991, Montgomery 1999). This spatial variability can influence the quantity and quality of allochthonous detritus (Pringle et al. 1988) over relatively small longitudinal scales. For example, patchiness in riparian tree cover can influence the composition, transport, retention, and storage of detritus (Johnson and Covich 1997). However, most studies of longitudinal patterns in organic matter flow have investigated changes over increases in stream order (e.g., Vannote et al. 1980, Minshall et al. 1983, Naiman et al. 1987, Minshall et al. 1992). Moreover, most of these

studies used single, small (<100 m) reaches to represent the ecosystems of entire stream orders.

Very few studies have quantified plant litter dynamics in small streams bordered by natural non-forested, herbaceous-dominated riparian zones (Xiong and Nilsson 1997, Gurtz et al 1988, Scarsbrook and Townsend 1994). Despite recognition of herbaceous plants as potential inputs to streams during floods (Gurtz et al. 1988, Gregory et al. 1991) few studies explicitly include them as a source of organic input (Gurtz et al. 1988, Bilby and Bisson 1992). Moreover, in a synthesis of organic matter budgets for 35 streams, Webster and Meyer (1997) indicated that floodplain particulate inputs were one of the most frequently missing components of stream ecosystem organic matter budgets.

Decomposition rates of detritus are slower in tissues with high carbon (C) to nitrogen (N) ratios and high concentrations of lignin. Consequently, material like wood and needles tend to have relatively long residence times in streams (Sedell et al. 1975, Triska et al. 1975, Anderson et al. 1978, Melillo et al. 1983). In contrast, decomposition rates of herbaceous plants are relatively fast (Webster and Benfield 1986). Therefore, herbaceous CPOM may have shorter in-stream residence times, and be fragmented to FPOM at faster rates than more recalcitrant tissues.

Headwater streams flowing through intact coniferous forests of the Pacific Northwest (PNW) often have characteristics which tend to stabilize carbon flow: they receive and store large quantities of recalcitrant woody material (particularly large wood) and needles, have low surface water and plant tissue nitrogen concentrations, and are highly physically retentive of particulate organic matter (Triska et al. 1982, 1984; Minshall et al. 1983, 1992). However, many headwater streams in the western mountains

alternately flow through coniferous forests and open, seasonally flooded riparian meadows. Studies in meadows have included only qualitative information on stream-riparian organic matter interactions. However, plant biomass and productivity in montane riparian meadows can be quite high: above-ground biomass in near-stream sedge-dominated (*Carex* spp.) communities can be over1000 grams/ m^2 (Otting 1998), a quantity at the high end of estimated litterfall inputs to streams throughout the temperate zone (Benfield 1997). Yet, interaction between this relatively large pool of organic matter and streams has not been studied.

Long-term reference reaches on two headwater streams in the Blue Mountains of Oregon provided an opportunity to study inputs and movement of CPOM in relatively undisturbed coniferous forests and downstream floodplain meadows. Studies at these sites have focused on the structure and biomass of the forests (Case 1995), relationships between shallow groundwater gradients and meadow plant species composition (Otting 1998), and biogeochemical processes at the stream-riparian meadow interface (Dwire et al 2000). Current research on organic matter flow at these sites indicates that short-term retention of CPOM is significantly higher in the forests than in meadows during spring snowmelt flooding, suggesting lower storage potential in the meadows (Chapter 3).

The objectives of our study were to estimate coarse particulate organic matter (CPOM) inputs, transport, and storage in two headwater streams. We compared processes of detrital import and movement in geomorphically constrained coniferous forest reaches with unconstrained floodplain meadow reaches. In particular, we examined litterfall and lateral (gravity and wind) input versus spring flooding as dominant vectors of CPOM import. We hypothesized that the relative significance of

seasonal flooding in detrital import and processing would be greater in the meadow floodplains than in the forests. We also analyzed CPOM for carbon and nitrogen concentrations to estimate total particulate inputs of these elements and to calculate C:N ratios. Specifically, we were interested in differences in C:N ratios of dominant CPOM components. We were also interested in temporal and longitudinal patterns in CPOM movement, specifically if transport rates differed among reaches during seasonal flooding and if CPOM storage changed along the longitudinal gradients.

METHODS

Study sites

The study sites are located along West Chicken Creek (45°3'17"N, 118°24'11"W) and Limber Jim Creek (45°06'15"N, 118°19'41"W), both second-order tributaries to the Upper Grande Ronde River in the Blue Mountains of northeastern Oregon (Fig. 1). The sites occur within the Wallowa-Whitman National Forest, approximately 40 km. southwest of La Grande. Geology of the study streams consists largely of quaternary alluvium underlain by Columbia River Basalts (Ferns and Taubeneck 1994). Soils at all sites are entisols (Dwire et al. 2000) largely composed of ash derived from volcanic eruptions in the Cascade Mountains (Harward and Youngberg 1970, Geist and Strickler 1978). Mean annual precipitation is 540 mm, the majority of which occurs as snowfall from November to May (PNW Forest Research Laboratory, La Grande, Oregon). Spring snowmelt occurs between April and June produces the peak discharge in the hydrographs of these streams (File data, USFS, La Grande)(Appendix A). Both streams are similar in

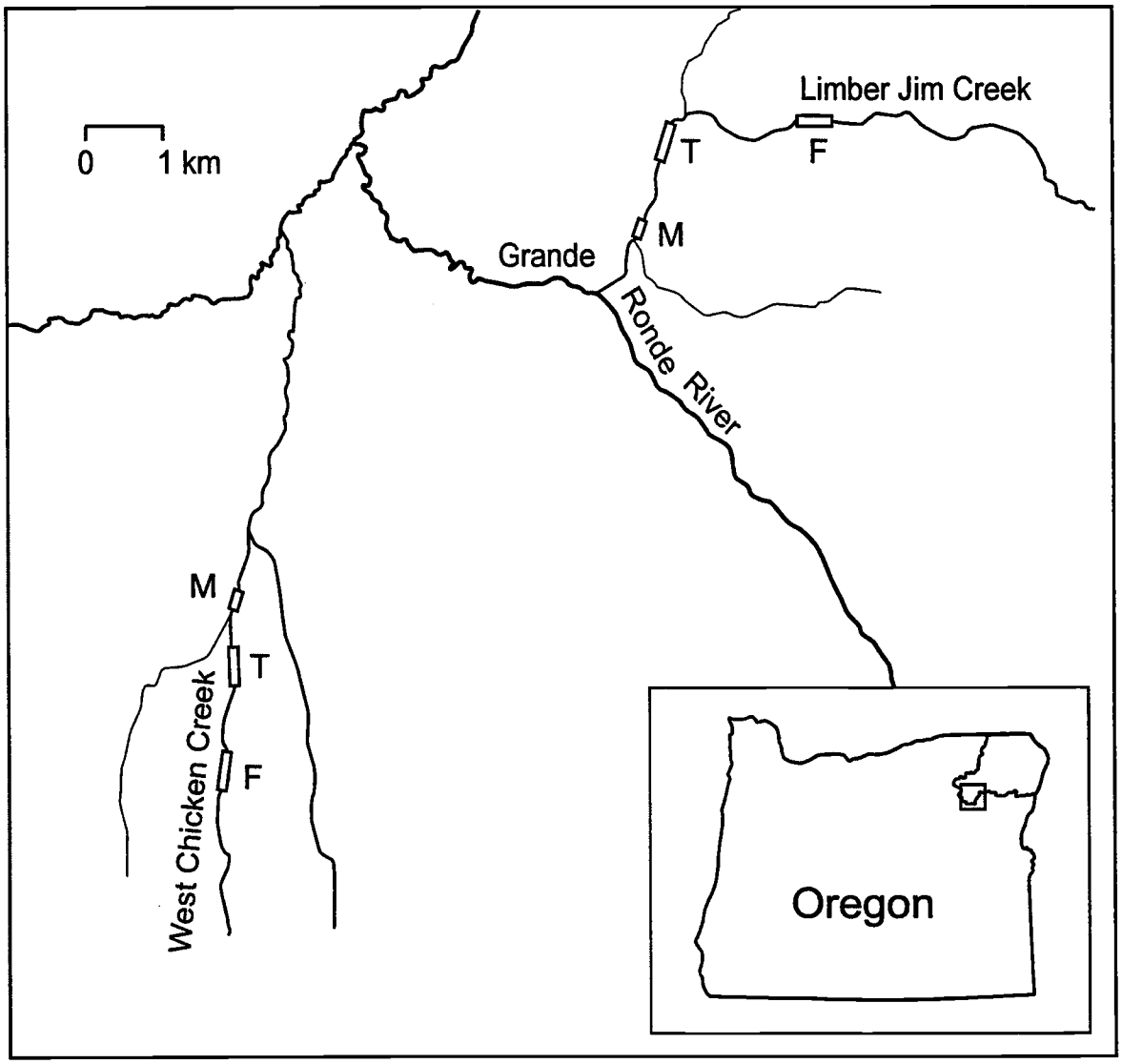

Figure 1. Study area showing forest (F), transition (T), and meadow (M) study reaches of West Chicken Creek and Limber Jim Creek.

Table 1. Characteristics of the study streams from 1997 - 1998.

	West Chicken Creek			Limber Jim Creek		
	Forest	Transition	Meadow	Forest	Transition	Meadow
Elevation (m)	1395	1361	1330	1396	1332	1311
Distance downstream (km)	4.5	6.0	6.9	5.7	8.0	9.2
Drainage area (km^2)	--	--	22	--	--	34
Gradient (%)	3.2	3.0	1.8	3.8	2.0	1.8
Valley width (m)	49	55	97	36	56	77
Discharge (cms)	0.01 - 0.6	--	0.03 - 1.0	0.07 - 1.8	--	0.1 - 2.5
Baseflow stream width (m)	1.5	1.3	1.2	2.9	3.6	2.8
Highflow stream width (m)	4.2	--	11.9	5.9	--	6.2
Baseflow thalweg depth (m)	0.11	0.22	0.26	0.2	0.25	0.3
Highflow thalweg depth (m)	0.27	--	0.6	0.44	--	0.55
Tree canopy cover (%)	77.8	12.9	2.4	79.1	17.1	4.3

(-- data not collected)

elevation, gradient, and canopy cover, but differ in drainage area, discharge, and channel morphology (Table 1).

We selected a 500-m reach (valley length) within an upstream forest segment and a 250-m reach in the downstream meadow segment of each stream. The meadow study reaches in both streams occur within cattle exclosures. An additional 500-m reach was selected at a longitudinally intermediate location between forest and meadow reaches (Fig. 1). Channel morphology generally is constrained in the forest segments and unconstrained in the meadow segments. Valley width approximately doubles in the meadow floodplains and riparian soils become progressively dominated by alluvial silts and clays downstream (Dwire et al. 2000). The dominant channel substrates are gravels and cobbles in all reaches.

Overstory vegetation in the forests is composed of 90 year old stands of coniferous trees, primarily Engelmann spruce (*Picea engelmanii*) which accounts for ~70% of conifer stem basal area (Case 1995). Other important conifers include Douglas-fir (*Pseudotsuga menziesii*) and western larch (*Larix occidentalis*). Mountain alder (*Alnus incana*)occurs almost continuously along the stream edge along Limber Jim Creek but is distributed in small clumps along West Chicken Creek (Case 1995). Within the active channel the understory shrubs *Ribes hudsonianum* and *R. lacustre* occur along with a variety of herbaceous plants.

Near-stream meadow plant communities are dominated by the common riparian sedges *Carex aquatilis, C. nebrascensis, C. utriculata,* and *C. lanuginosa.* Tree canopy cover is low in the meadows (<5%)(Table 1) but scattered patches of conifers (primarily *Pinus contorta*) are present. Also, alder and willow (*Salix* spp.) are common along the meadow section of Limber Jim Creek. Gravel bars dominated by grasses and forbs are common at Limber Jim meadow, but are virtually absent at West Chicken meadow. Riparian vegetation occurring between the downstream end of the forest reaches and the upstream end of the meadow reaches is transitional, consisting of a patchy *P. contorta* and alder overstory with an herbaceous, largely graminoid, understory.

The largest riparian trees in the forest sections were selectively logged in the 1970's. However, these sites are similar in biomass, structure, and species composition to riparian forests in the basin that have never been logged (Case 1995). Cattle were grazed in the meadows until exclusion in 1995 at West Chicken Creek and until 1978 at Limber Jim Creek; current land use is restricted to recreational activities. Populations of federally listed salmonids inhabit both streams and management of adjacent riparian areas

is considered critical to their survival (National Marine Fisheries Service; USFS, La Grande).

Physical variables

The USFS La Grande District monitors discharge at the downstream end of the meadow reach of both streams. Discharge records were continuous for the August 1997 - October 1998 study period at Limber Jim Creek but some data are missing for West Chicken Creek. We measured discharge in the forest reaches at three locations and on seven dates using a flow meter (Swoffer 2100). Stream width measurements (n >100) were also taken at all study sites during high-flow conditions in 1997 and during base-flow in 1998.

Litterfall and lateral inputs

To estimate litterfall and lateral CPOM inputs to the forest reaches we installed ten 0.19-m^2-frame litterfall and ten lateral traps in paired random locations and collected contents monthly from August 1997 - November 1998. Traps were constructed of nylon netting (<1 mm mesh) through which water rapidly drained. Litterfall traps were suspended 1 m over the stream to avoid damage during high-flows. Lateral traps were placed on one side of the stream within 1 m of litterfall traps above high flow margins and were positioned facing up-slope away from the channel. Litterfall and lateral inputs were calçulated as inputs per m^2 of stream surface and inputs per meter of stream length

following the methods of Conners and Naiman (1984). For stream surface calculations, lateral movement rates (g/ m/ time) were multiplied by two to account for both sides of the stream and then divided by average stream width. For the stream length calculations, litterfall rates were multiplied by average stream width. Most *Ribes* shrubs occurred in the active channel beneath the height of litterfall traps but also between the stream and lateral traps. Leaf inputs from *Ribes* ($g \cdot m^{-2} \cdot yr^{-1}$) were estimated by removing all leaves from ten randomly selected *R. hudsonianum* and *R. lacustre* plants just prior to abscission (September 1997) and then multiplying biomass by average *Ribes* densities (number/m^2) estimated by Case (1995). Samples were air dried and stored in paper bags until laboratory analysis.

In the laboratory all samples were fractionated into seven categories: herbaceous material; alder bud scales; broad leaves; lichens; needles; cones, twigs, bark, and wood (CTBW; Triska et al. 1984), and miscellaneous (flowers, sap, unidentifiable particles, etc.). All samples were then oven dried at 60°C and weighed. Composite sub-samples of each category ($n = 4$) from each stream were dried at 60°C to a constant weight, weighed, ashed at 550°C for >10 hrs, and re-weighed to determine ash free dry mass (AFDM).

In July, 1998 we installed five litterfall and five lateral traps in each meadow reach and collected and analyzed contents following above methods. However, in August 1998 cattle intruded into West Chicken Creek meadow and destroyed the traps, thus precluding our ability to continuously sample inputs into this reach for summer 1998. Traps were reinstalled ~ three weeks later. Data for the meadow reaches are continuous from September- November 1998. Material was not fractionated into tissue types.

High-flow inputs

In the forest and meadow reaches, we estimated allochthonous CPOM input occurring during spring high-flows by destructively sampling herbaceous material and litter in paired plots along ten randomly placed transects within the active channel before and after high-flows (*pre-* and *post-flood*). Delineation of active channel width was based on ocular estimates of potential high-flow stream widths indicated by abrupt changes in topography and vegetation. Transects were positioned perpendicular to the direction of stream flow on one side of the stream. At the end of the growing season in 1997 (late September), collection plot locations were established at three positions along each transect: stream edge, mid-active channel, far-edge of active channel for a total of 30 plots per reach. All rooted herbaceous plants and unattached litter within plot frames (0.062 m^2) were collected to ground surface. Care was taken to avoid inclusion of any organic soil material in litter collections. After spring high flow waters had completely receded (late June 1998) we sampled material in plot frames placed directly within 1 m upstream of the original samples ($n = 30$). Current year's herbaceous growth, green broad leaves, and green needles were all removed from samples in the field.

In the laboratory, samples were separated into four categories: forbs (includes dicots and non-graminoid monocots), graminoids (grasses, sedges, rushes), herbaceous litter, and non-herbaceous litter. Forb and graminoid litter were not separated because the former was insignificant in abundance compared to the latter. Samples were dried at 60°C and weight to estimate mass. Sub-samples of each category from both forest and

meadow reaches (n = 5 per category) were analyzed to determine AFDM. All herbaceous biomass values are reported as AFDM.

Potential herbaceous allochthonous CPOM was estimated with the calculation: pre-flood herbaceous biomass - post flood dead biomass = potential allochthonous input. This calculation does not account for leaching and decomposition losses that may have occurred between sampling in September 1997 and the onset of spring flooding (~ 6 months later). From late fall to early spring 1997 much of the active channel within the forest reaches was covered in solid ice or snow. However, snow accumulation in the meadows was patchy and underwent several freeze-thaw sequences (*personal observation*). Several studies have documented decomposition under snow cover (Bleak 1970, O'Lear and Seastedt 1994, Arp et al. 1999) and high microbial activity during snowmelt (Brooks et al. 1998, Lipson et al. 1999). Therefore, to account for potential decomposition losses before flooding we applied the model:

$$\ln(x_t/x_0) = -kt$$

where x_0 is the original mass of litter, x_t is the amount of litter remaining after time t (in years), and k is the decomposition constant (yr^{-1}) (Wieder and Lang 1982). We averaged k values taken or calculated from published studies on *Carex* decomposition conducted in wetlands (Arp et al. 1999, Verhoeven and Arts 1987, Aerts and De Caluwe 1997, Thorman and Bayley 1997), yielding an approximate mean $k = 0.5$. We also applied an average percent leaching loss of 10% taken from literature values on *C. aquatilis* (Thorman and Bayley 1997) and *C. rostrata* (= *utriculata*)(Ohlson 1987). We calculated the amount of combined (live plus dead) *Carex* material remaining after $t = 0.5$ yr. by

first applying the 10% leaching loss to our estimates of standing sedge biomass and entering the remaining material into the decomposition model. We assumed that unattached litter had undergone substantial leaching prior to sampling, and therefore did not apply a leaching loss. We subtracted the mass remaining in the spring samples from this value to estimate potential allochthonous inputs. The same adjustments were applied to forb material and to forest herbaceous biomass averages.

Carbon and nitrogen analysis

Composite samples of alder leaves (n = 14), needles (n = 44), CTBW (n = 31), lichens (n =8), *Ribes* leaves (n = 12), and miscellaneous (n = 8) from the forest sites were analyzed for carbon and nitrogen concentrations. For both forest sites, samples were composited by combining the entire sample of each plant category from several (4-7) randomly selected traps. Samples of needles, CTBW, and lichens were also separated by the season of sample collection. Randomly composited sub-samples of pre-flood forbs from the forest (n = 4) and meadow sites (n = 4) were also analyzed. Randomly selected samples from four transects of pre-flood living (n = 12) and dead (n = 12), and post-flood dead graminoid tissues (n = 12) from the meadow sites were rinsed with distilled water for about 60 seconds to remove flood-deposited silt and sand before analysis. Samples were ground using a Cyclone Udy Mill and then analyzed by the flash combustion method using a Carlo-Erba NA1500 NCS analyzer (Fisons Instruments, Danvers, Massachusetts). To estimate particulate carbon and nitrogen inputs, average

concentrations were multiplied by the average dry mass input value of each plant category.

Transport

CPOM transport was estimated in forest, transition, and meadow reaches by collecting drift during periods of high-, intermediate-, and low-discharge (Appendix A). We used torpedo-shaped drift nets with a 0.09 m^2 opening and 0.5 mm mesh. The net was positioned in the thalweg at the upstream and downstream ends of each forest and meadow reach and in the middle of the transition reach, with three replicates per location and sampling date (n = 15/ stream/date). Nets were immersed for 15 minutes during low- and intermediate discharge and for 5 minutes during high-discharge. To estimate potential influences of tributaries on longitudinal patterns of transport, additional samples (n = 3) were collected in the major tributaries to both streams ~ 4 m upstream of the confluence location during one day of high flow. Drift nets were positioned within the middle of the water column but at least 2 cm above the substratum to avoid sampling benthic material. The volume of water passing through the net was measured with a flow meter positioned about 10 cm in front of the net during each collection. Visible macroinvertebrates were removed in the field. The samples were kept cold until processing within 2 - 4 days. All samples were dried at 60°C, weighed to a constant mass, ashed at 550°C for 12 hours, and re-weighed. Transport rates were then calculated by multiplying concentration by discharge.

Storage

Within forest, meadow, and transition reaches of both streams, we measured all large wood (>10 cm diameter) and counted all visible small wood (1-10cm diameter and >30 cm in length) occurring within three randomly selected 50-m sites, for a total of nine sites at each stream. We conducted two measurements of wood: volume occupying the bankfull channel above or outside the base-flow wetted channel, and volume within the wetted channel at base-flow (Raikow et al. 1995). Wetted stream widths and active channel widths were measured in each reach and then multiplied by 50 m to calculate base- and high-flow surface areas. Wood volume was calculated using the formula:

$$V = (\pi (d_1^2 + d_2^2) L)/ 8$$

where d_1 and d_2 are the end diameters of the log and L is the length. We obtained mass estimates for large and small wood within a reach by multiplying an assumed specific gravity of conifer wood (0.4 Mg/ m^3) by volume per unit area (Lienkaemper and Swanson 1987). Based on average dimensions of small wood measured in the forest reach of West Chicken Creek, we calculated small wood mass for all sites by applying the average dimensions of small wood (4 cm in diameter and 50 cm in length) to each counted piece and then multiplying by 0.4 Mg/ m^3.

In September 1999, before the majority of leaf fall and during base-flow, benthic organic matter (BOM) was estimated at all sites within geomorphically representative 100 m reaches with the use of a 0.09-m^2 (250 μm mesh) surber sampler. Samples were collected every 10 m (moving upstream) in a repeating pattern (left, middle, right) within the wetted perimeter of the stream ($n = 10$). At each sampling location, the major

geomorphic feature (riffle, glide, pool) was noted. Benthic material was obtained by vigorously mixing the substrate within the surber frame to a depth of ~ 10 cm for <30 sec. and allowing material to float into the net. Material was size-fractionated in the field with a 1-mm sieve while rinsing fine material into a bucket. Large rocks, macroinvertebrates, and live plant material were rinsed over the sieve and removed. Coarse material (CBOM) was collected and stored in plastic bags. Fine material (FBOM) in the bucket was rewetted and poured into plastic bags. In the laboratory, samples were oven dried, weighed, ashed, and reweighed. Large CBOM samples were sub-sampled (n=3) for determination of AFDM.

Data analysis

Differences between pre- and post flood herbaceous samples and associated carbon and nitrogen concentrations were tested with paired t-tests and Fisher's LSD multiple comparison tests. Transport rates (kg/day) were log-transformed to normalize distributions. Transport concentrations were regressed against discharge using simple-linear regression. Because of the non-normality of BOM data, differences in total BOM among reaches were tested using non-parametric procedures (Kruskal-Wallis test; Zar 1984) with SPSS (Version 9.0.0, 1998). Paired t-tests were performed on BOM data after grouping by reach and channel unit type. Parametric analyses were conducted using SAS (version 6.12, SAS Institute Incorporated, Cary, North Carolina, USA).

RESULTS

Litterfall and lateral inputs

Total litter input rates to the forest sites ranged from 0.09 - 0.15 $g \cdot m^{-2} \cdot day^{-1}$ in the spring to peaks of 1.05 - 1.30 $g \cdot m^{-2} \cdot day^{-1}$ in autumn during deciduous leaf abscission. Average monthly litterfall input rates greatly exceeded lateral input rates for the August 1997 to November 1998 period (Fig. 2). Average total inputs per area of stream surface in the forests were 173 $g \cdot m^{-2} \cdot yr^{-1}$ at West Chicken Creek and 162 $g \cdot m^{-2} \cdot yr^{-1}$ at Limber Jim Creek. Over 80% of annual litter inputs consisted of litterfall (Fig. 2). Average total inputs per meter of stream length were an average of 271 g/yr at West Chicken Creek and 479 g/yr. at Limber Jim Creek.

Mean daily litter inputs to the forest reaches (0.72 - 0.86 g/m^2) during peak litterfall in autumn, 1998 were >60 times the input to the meadow reach of West Chicken Creek (~ 0.01 g/ m^2) and >8 times the input to the meadow reach of Limber Jim Creek (~ 0.11 g/ m^2)(Fig. 3). Daily input rates of litter to the meadows were averaged for June - November 1998 to calculate estimates of annual litterfall and lateral inputs. Using an average of 0.115 $g \cdot m^{-2} \cdot day^{-1}$ for Limber Jim Creek and an average of 0.012 $g \cdot m^2 \cdot day^{-1}$ for West Chicken Creek (Fig. 3), we estimated that annual litterfall and lateral inputs were 3.7 to 40-fold higher in the forests than in the meadows (Table 2).

Litterfall and lateral inputs differed compositionally during the August 1997 - September 1998 period (Fig. 4). The annual pattern of litterfall in the forests was characterized by marked seasonality in input rates of alder leaves in the fall and conifer

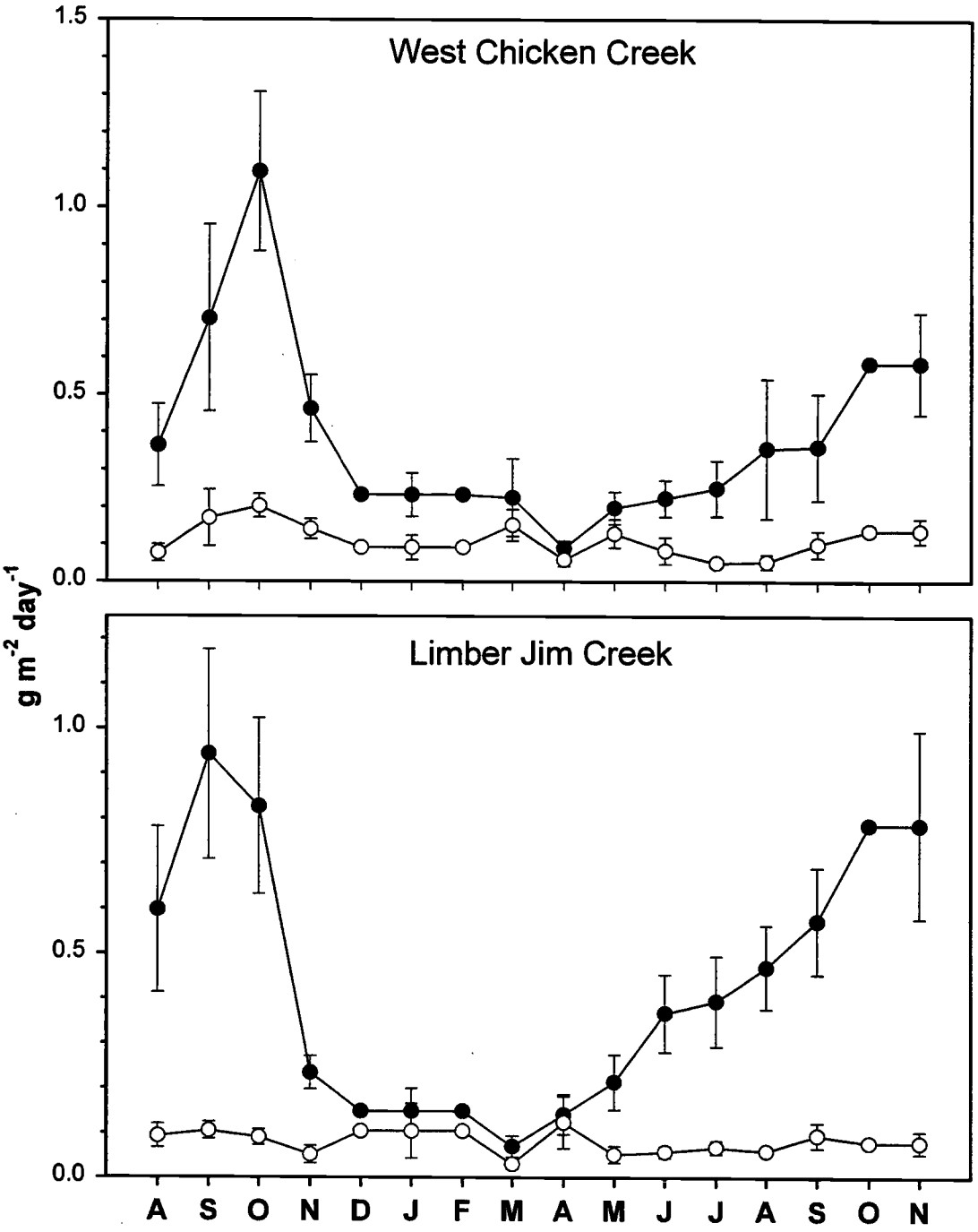

Figure 2. Litterfall (solid circles) and lateral (open circles) input rates to the forest reaches of the study streams for the August 1997-November 1998 period. Points are averages of 6-10 traps and vertical bars are one standard error. Trap contents were collected once for the December- February and the October-November periods.

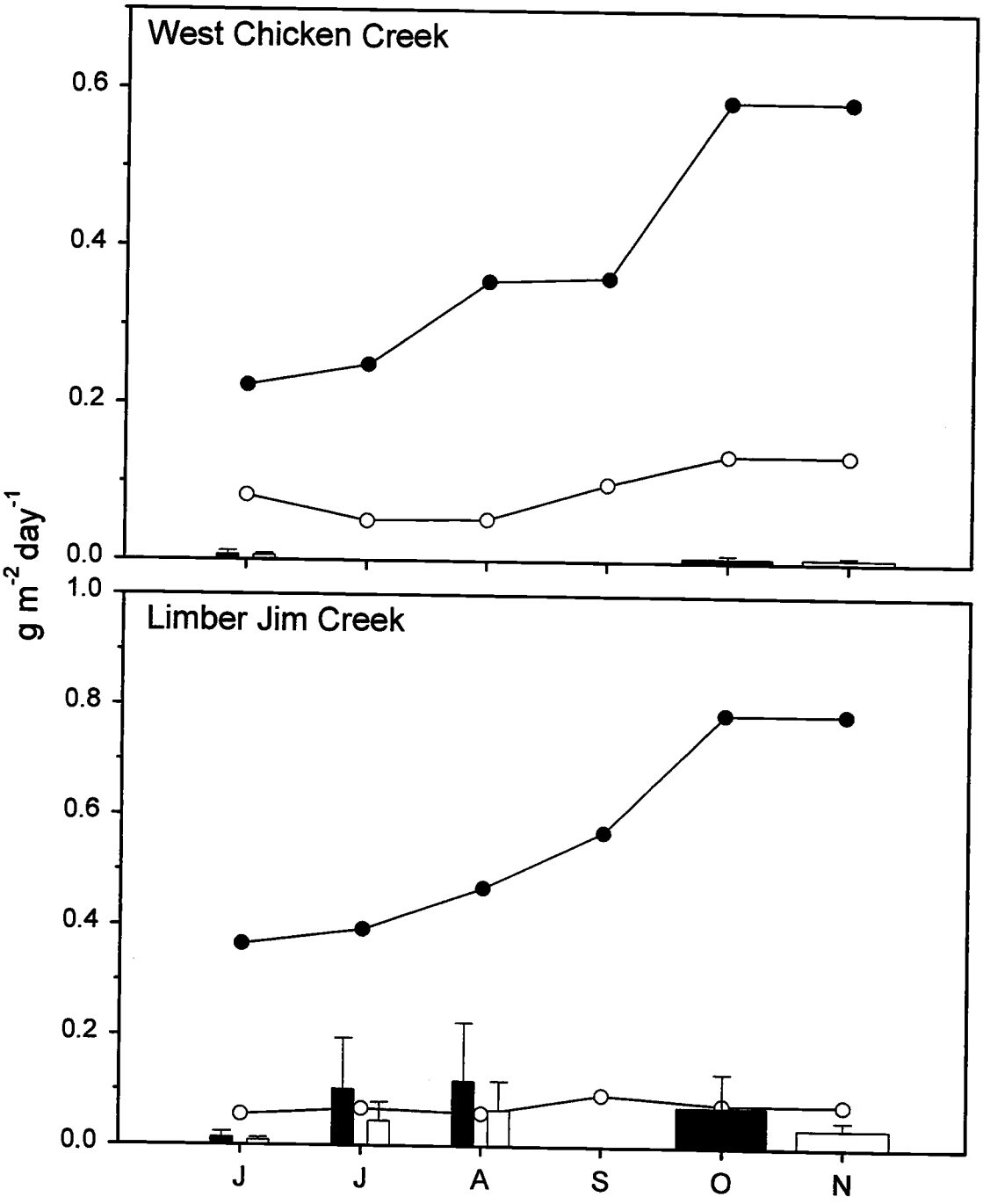

Figure 3. Comparison of litterfall (black dots and bars) and lateral input rates (white dots and bars) in forest (lines) and meadow (bars) reaches of of the study streams for the June 1998 to November 1998 period. Bars are averages ($n = 5$) and error bars represent one standard error. Larger bars represent litterfall and lateral inputs for October and November.

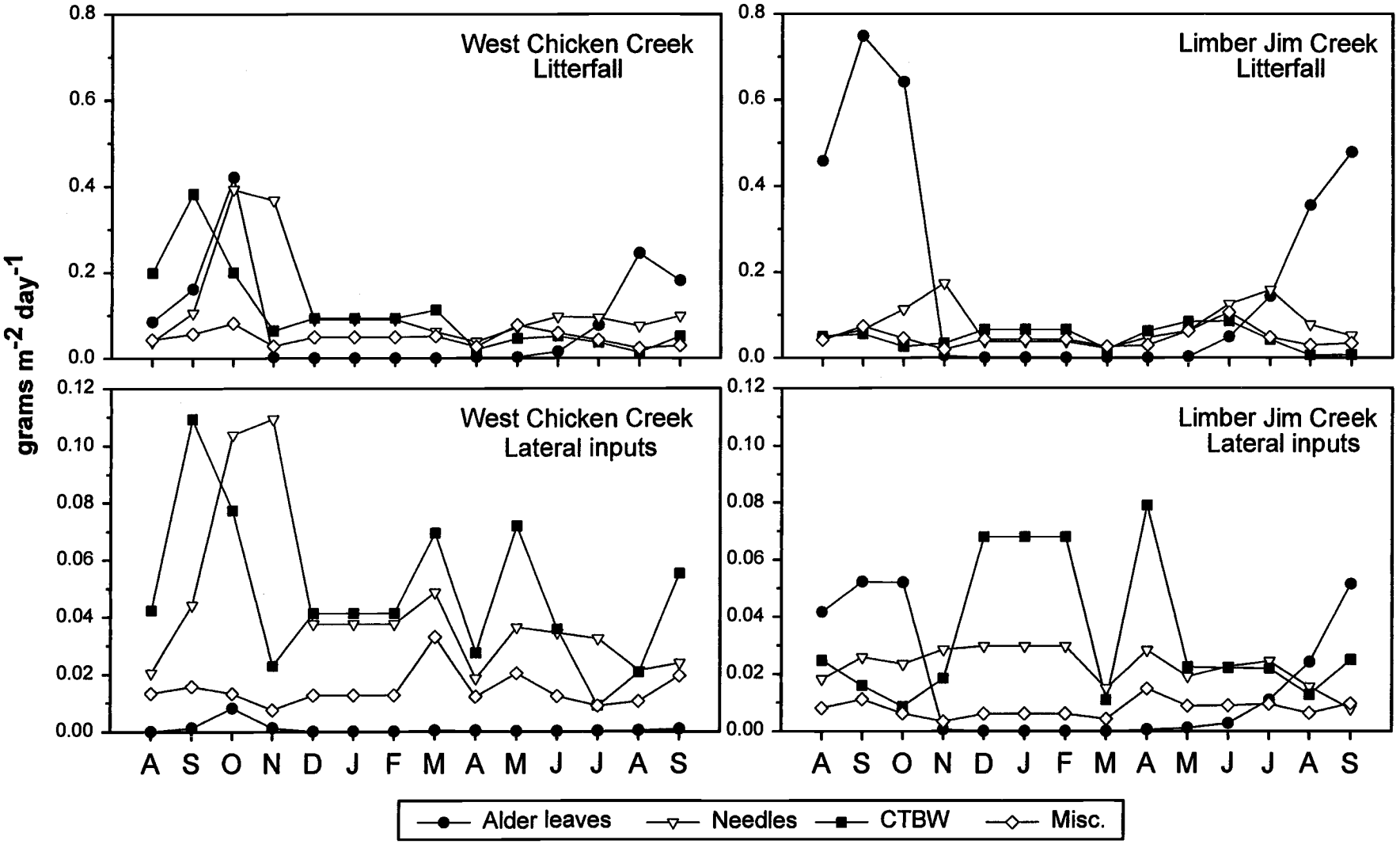

Figure 4. Composition of litterfall and lateral inputs to the forest reaches for the August 1997 to September 1998 period. Note difference in scale among graphs. Each point is a mean of 6-10 traps. CTBW = cones, twigs, bark, and wood.

needles associated with larch needle drop in the late fall (Fig. 4). At West Chicken Creek, total litterfall (131 $g \cdot m^{-2} \cdot yr^{-1}$) was dominated by needles (37%), CTBW (27%), and alder leaves (23%). Total litterfall (128 $g \cdot m^{-2} \cdot yr^{-1}$) to Limber Jim Creek was dominated by alder leaves (54%), followed by needles (21%) and CTBW (17%). Average total input from *Ribes* shrubs was 1.38 $g \cdot m^{-2} \cdot yr^{-1}$ at West Chicken Creek and 0.99 $g \cdot m^{-2} \cdot yr^{-1}$ at Limber Jim Creek. Lateral input rates exhibited less seasonality than litterfall and were highly variable through time, particularly in CTBW (Fig. 4). Total annual lateral inputs (41 and 30 $g \cdot m^{-2} \cdot yr^{-1}$) were dominated by CTBW (43% and 37%) and needles (43% and 29%) at West Chicken Creek and Limber Jim Creek, respectively.

High-flow herbaceous inputs

In late September 1997, total aboveground herbaceous biomass within the active channel in the meadows was an average of 645 g/ m^2 at West Chicken Creek and 400 g/ m^2. Herbaceous biomass was much lower in the forest reaches: an average of 82 g/ m^2 at West Chicken Creek and 70 g/ m^2 at Limber Jim Creek. Average post-flood total herbaceous biomass was significantly lower ($P<0.001$) than pre-flood biomass at all sites (Fig. 5). Total herbaceous biomass remaining after spring high-flows was < 16% of pre-flood estimates in the forest sites but was ~30% of pre-flood estimates in the meadow sites. However, there were no significant differences ($P>0.10$) between pre-and post-flood samples in herbaceous litter and non-herbaceous litter biomass.

Table 2. Summary of annual CPOM, carbon, and nitrogen inputs (g m^{-2} yr^{-1}) to forest and meadow study reaches of West Chicken Creek (WC) and Limber Jim Creek (LJ) for the August 1997 to November 1998 period. High-flow input estimates are presented as both decompostion-adjusted (above) and non-adjusted values (below). Totals are sums of litterfall and lateral inputs and decomposition-adjusted high-flow inputs (g m^{-2} yr^{-1}). Inputs per meter of stream length were calculated using both average transect widths and observed high-flow stream widths. Numbers in parentheses are one standard error.

	Forest		Meadow	
	WC	LJ	WC	LJ
Litterfall and lateral				
CPOM	160.9 (47.9)	148.2 (42.7)	4	40
Carbon	83.9 (25)	77.2 (22.2)	2	20
Nitrogen	1.6 (0.5)	2.6 (0.7)	0.03	0.7
High-flow				
CPOM	50.1 (6.9)	38.7 (8.8)	262.7 (50.4)	174.2 (32.4)
	73.7 (10.1)	58.9 (12.5)	444.5 (65.1)	284.9 (41.2)
Carbon	18.5 (2.5)	14.3 (3.2)	90 (17.4)	65.2 (12.1)
	27.3 (3.7)	21.8 (4.6)	153.8 (22.5)	106.6 (15.4)
Nitrogen	0.5 (0.07)	0.4 (0.09)	2.7 (0.5)	1.5 (0.3)
	0.8 (0.1)	0.6 (0.1)	4.5 (0.7)	2.5 (0.4)
Total inputs				
CPOM	211	186.9	266.7	214.2
Carbon	102.4	91.5	92	85.2
Nitrogen	2.4	3.2	4.5	3.2
Loading per meter of stream				
Transect	392	621	1182	778
Stream	382	553	2816	592

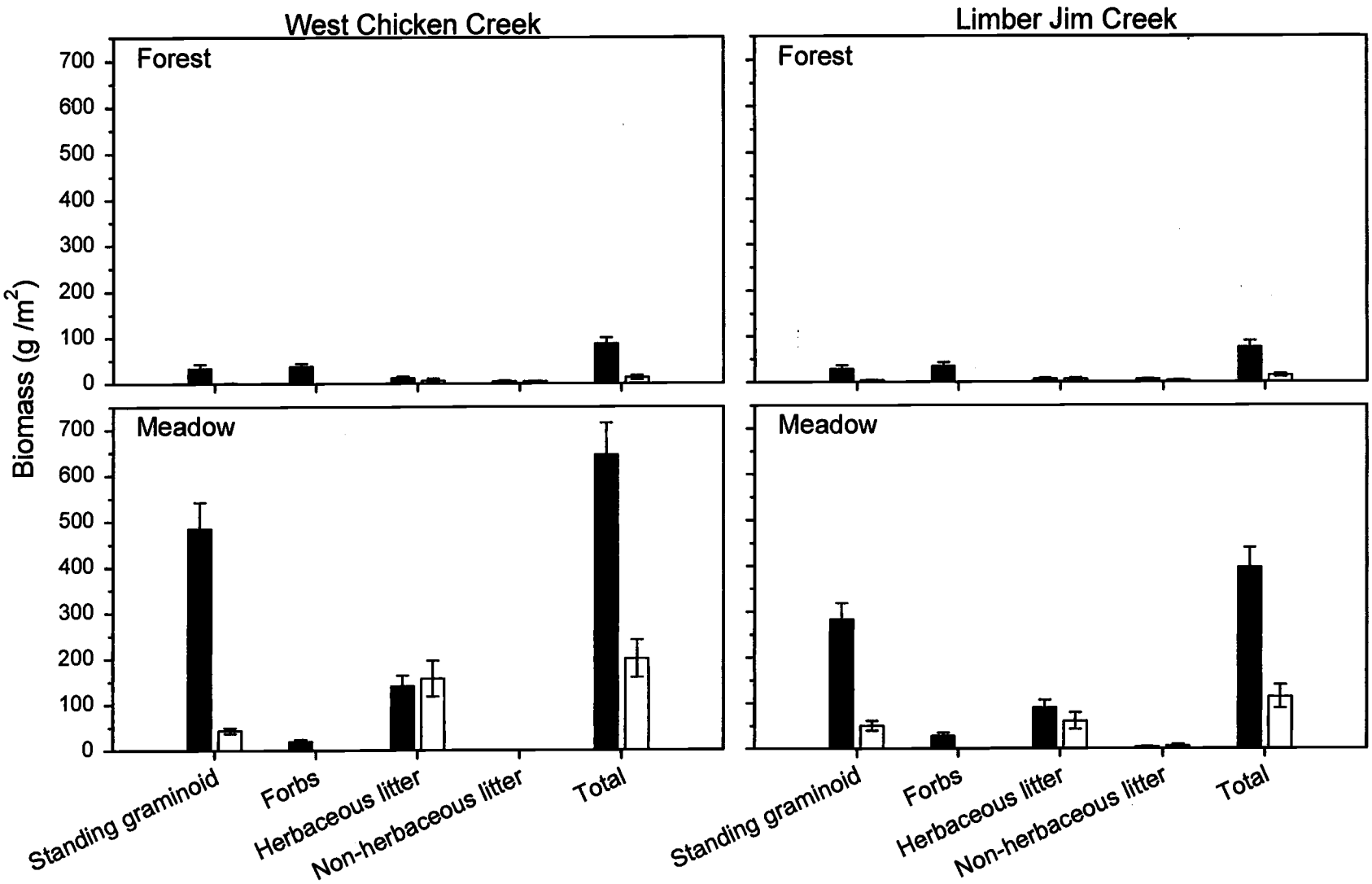

Figure 5. Pre-flood (solid bars) and post-flood (open bars) herbaceous biomass occuring within the active channels of the forest and meadow study reaches. Bars are averages (n = 30) and error bars are one standard error.

We calculate that 174 – 445 g · m^{-2}·yr^{-1} of herbaceous material was fluvially imported into the meadow reaches compared to 39 - 74 g · m^{-2}·yr^{-1} in the forest reaches (Table 2). Adjusting for potential leaching and decomposition reduced pre-flood herbaceous biomass estimates by an additional ~30%. There were no significant differences among plot locations along transects (stream edge, mid active channel, far edge)(P>0.10, Kruskal-Wallis test). Therefore, we added litterfall and lateral CPOM loading estimates to the product of active channel inundation (active channel width - base-flow stream width) and average herbaceous inputs per m^2 to calculate inputs per meter of stream (loading). Loading was calculated using both average transect widths and observed high-flow stream widths (Table 2). Although all plots were inundated during high-flow, transect widths were wider than observed stream widths for all reaches except for the meadow reach of West Chicken Creek. At this site, high-flow stream widths were over twice as wide as transect widths. Consequently, the loading estimate based on stream width at this site represents an extrapolated *potential* input (Table 2).

C and N inputs and C:N ratios

C and N concentrations of CPOM inputs varied widely among components and between forest and meadow reaches. In the forest reaches, C concentrations ranged from 42% in *Ribes* leaves to 51% in CTBW; N ranged from 0.7% in needles to 2.7% in alder leaves (Table 3). In the meadow reaches, organic matter content (% AFDM), and both C and N concentrations of graminoid tissues (primarily *Carex*) varied significantly from live standing material to post-flood litter (Table 4). C concentrations of all graminoid

Table 3. Summary of C and N concentrations (%), C:N ratios, and percent of total annual input of all CPOM input components to forest and meadow reaches of the study streams. Also included are the weighted C:N ratios of total inputs to each reach. Numbers in parentheses are one standard error.

CPOM	n	C	N	C:N	% of inputs
West Chicken Creek					
Forest					
Needles	16	48.16 (0.09)	0.73 (0.09)	66.63 (2.30)	28
CTBW	12	50.16 (0.15)	0.82 (0.15)	63.77 (4.13)	27
Lichen	4	43.48 (0.28)	1.42 (0.28)	30.65 (0.53)	6
Misc	4	47.96 (0.58)	1.84 (0.17)	26.72 (2.40)	4
RIHU	3	42.54 (0.52)	1.95 (0.52)	22.01 (1.40)	0.4
RILA	3	42.61 (0.25)	1.77 (0.09)	24.16 (1.24)	0.3
Forbs	4	41.02 (0.68)	1.11 (0.08)	37.58 (2.79)	12.3
Alnus leaves	4	48.45 (0.72)	2.30 (0.18)	21.38 (1.35)	11
Graminoids	--	36.02	0.95	39.96	11
Total*	--	45.98	1.09	49.76	--
Meadow					
*Carex***	12	34.62 (0.99)	1.02 (0.09)	35.84 (1.42)	91
Forbs	4	41.22 (0.49)	1.59 (0.16)	26.81 (2.75)	7
Litterfall and lateral	--	48.06	0.89	59.16	2
Total	--	36.21	1.00	35.37	--
Limber Jim Creek					
Forest					
Needles	28	48.82 (0.16)	0.79 (0.03)	64.99 (2.82)	18
CTBW	19	50.76 (0.19)	0.97 (0.07)	56.66 (3.87)	17
Lichen	4	43.28 (0.42)	1.35 (0.08)	32.37 (1.73)	4
Misc	4	46.35 (0.47)	1.57 (0.05)	29.72 (1.40)	4
RIHU	3	42.64 (0.37)	2.23 (0.23)	19.63 (2.41)	0.4
RILA	3	42.40 (0.56)	1.64 (0.18)	26.57 (3.56)	0.1
Forbs	4	37.12 (1.84)	1.13 (0.09)	33.17 (2.53)	11.5
Alnus leaves	10	49.39 (0.25)	2.68 (0.06)	18.47 (0.36)	35.5
Graminoids	--	36.02	0.95	39.96	9.5
Total	--	45.79	1.55	37.61	--
Meadow					
Carex	12	37.42 (1.10)	0.87 (0.06)	44.08 (1.86)	74
Forbs	4	33.32 (1.89)	1.27 (0.04)	26.31 (1.64)	8
Litterfall and lateral	--	48.21	1.71	39.69	18
Total	--	38.3	1.01	41.87	--

* Total values represent the mean C, N, and C:N ratios of annual inputs calculated by summing the values of each component weighted for the percentage of the total inputs accounted for by that component. ** *Carex* values represent the chemistry of pre-flood tissues.

Table 4. Mean AFDM (n = 5), carbon (n = 12), and nitrogen (n = 12) concentrations (%) for *pre*-flood standing sedge material and litter and *post*-flood sedge litter in the meadow reaches of West Chicken Creek and Limber Jim Creek. Numbers in parentheses are one standard error.

	AFDM	Carbon	Nitrogen	C:N
West Chicken Creek				
pre-Standing	89.60 (0.37)[a]	43.30 (0.15)[a]	1.06 (0.03)[a]	41.18 (2.35)[a]
pre-Litter	60.83 (5.35)[b]	34.62 (0.99)[b]	1.02 (0.09)[a]	35.84 (1.42)[a]
post-Litter	53.41 (5.86)[c]	29.26 (1.77)[c]	0.81 (0.05)[b]	37.29 (2.79)[a]
Limber Jim Creek				
pre-Standing	89.58 (0.47)[a]	43.10 (0.33)[a]	0.97 (0.05)[a]	45.54 (1.93)[a]
pre-Litter	76.48 (4.02)[b]	37.42 (1.10)[b]	0.87 (0.06)[a]	44.08 (1.86)[a]
post-Litter	52.41 (8.07)[c]	30.55 (1.80)[c]	0.70 (0.03)[b]	43.48 (1.90)[a]

Superscripted letters indicate significant differences among tissue types within sites. Level of significance for AFDM and carbon is $P<0.01$ and $P<0.05$ for nitrogen.

tissue types were significantly different ($P<0.01$). Nitrogen concentration did not differ ($P>0.15$) between pre-flood tissues, but did differ ($P<0.05$) between pre- and post-flood tissues. To estimate herbaceous C and N inputs into the meadow reaches, we used *pre*-litter concentrations of sedges (Table 4) because these values incorporated potential belowground C and N translocation and terrestrial leaching that could have occurred prior to spring flooding. To estimate elemental inputs from forbs, we assumed the same proportional mass loss as in graminoid material by multiplying forb biomass values by 0.37 for C and 0.0105 for N. Forest graminoid inputs were calculated by using pre-flood meadow graminoid concentrations (Table 3).

Annual inputs of particulate C and N were similar between forest and meadow reaches, ranging from 85 to102 g/m^2 for C and 2.4 to 4.5 g/m^2 for N, but the sources of these inputs were very different (Table 2). Sources of C and N input tracked inputs of

Table 5. Comparison of mean C and N concentrations (%) and C:N ratios of major CPOM components for all sites combined. Numbers in parentheses are one standard error.

	n	C	N	C : N
Needles	44	48.58 (0.12)[a]	0.77 (0.02)[a]	65.59 (1.96)[a]
CTBW	31	50.53 (0.14)[b]	0.91 (0.05)[b]	59.42 (2.89)[a]
*Carex**	24	36.02 (1.11)[c]	0.95 (0.08)[b]	39.96 (1.72)[b]
Forbs	16	38.17 (1.04)[c]	1.27 (0.07)[c]	30.96 (1.64)[c]
Alnus	14	49.12 (0.28)[d]	2.57 (0.08)[d]	19.30 (0.56)[d]

Values with different superscripted letters within columns are significantly different ($P < 0.05$ for C between *Alnus* and needles, $P < 0.003$ for N between needles and CTBW, and $P < 0.001$ for all other differences).

* Chemistry values for *Carex* represent pre-flood litter means. Although C, N and C:N ratios of *Carex* differed significantly ($P = 0.02$) between streams, significance values for tests among other CPOM components were the same ($P < 0.001$) for both streams.

organic matter for all components but alder leaves which accounted for a disproportionate amount of forest N inputs. Alder leaves comprised the majority of annual particulate N input to the forest reaches (1.8 g/m^2 for 72% of input to Limber Jim Creek and 0.5 g/m^2 for 35% of input to West Chicken Creek). Needles accounted for 24% and 9% and CTBW accounted 22% and 8% of the remaining N inputs to West Chicken Creek and Limber Jim Creek, respectively (Table 2, Appendix D). In contrast, herbaceous material comprised 98% and 81% of C and N inputs to the meadow reaches of West Chicken Creek and Limber Jim Creek, respectively.

Carbon, N, and C:N ratios of total annual inputs to each site were calculated by adjusting for the proportion of different components in the total. Due to low C:N ratio alder leaf and herbaceous inputs, C:N ratios of total CPOM inputs were very similar between forest and meadow reaches (Table 3). However, there were significant

(P<0.001) differences in the mean C:N ratios of the major CPOM input components and between forest and meadow reaches (Table 5). From recalcitrant to labile, C:N ratios of CPOM components were arranged in the order: needles > CTBW > *Carex* litter > forbs > alder leaves.

Transport

Discharge for the 1997 - 1998 period ranged from ~0.001 - 1 $m^3 s^{-1}$ in West Chicken Creek and from ~ 0.05 - 2.5 $m^3 s^{-1}$ in Limber Jim Creek. Differences in organic matter transport reflected differences in discharge between the two streams: transport rates ranged from 0.003 - 1.7 kg/day in West Chicken Creek and from 0.08 - 22.9 kg/day in Limber Jim Creek. At high-flow, tributaries to the two streams contributed 0.03 kg/day to West Chicken Creek and 3.65 kg/day to Limber Jim Creek. Transport rates decreased downstream during high-flow despite tributary inputs in West Chicken Creek (Fig. 6C). During high flow at Limber Jim Creek, increased discharge due to a tributary resulted in significantly higher (P<0.001) CPOM transport rates in the transition reach than in forest and meadow reaches (Fig. 6D). During high- and intermediate flow, samples from all reaches in both streams were composed primarily of woody material and needles. However, during base-flow, some samples from the meadow reaches in both streams were composed of ~25% algae.

When all sampling dates were combined, mean transport rates (kg/day) of CPOM was significantly higher in the forest reach than in the meadow reach of West Chicken Creek (P< 0.0001) but not at Limber Jim Creek (P = 0.278)(one-tailed t-tests). However,

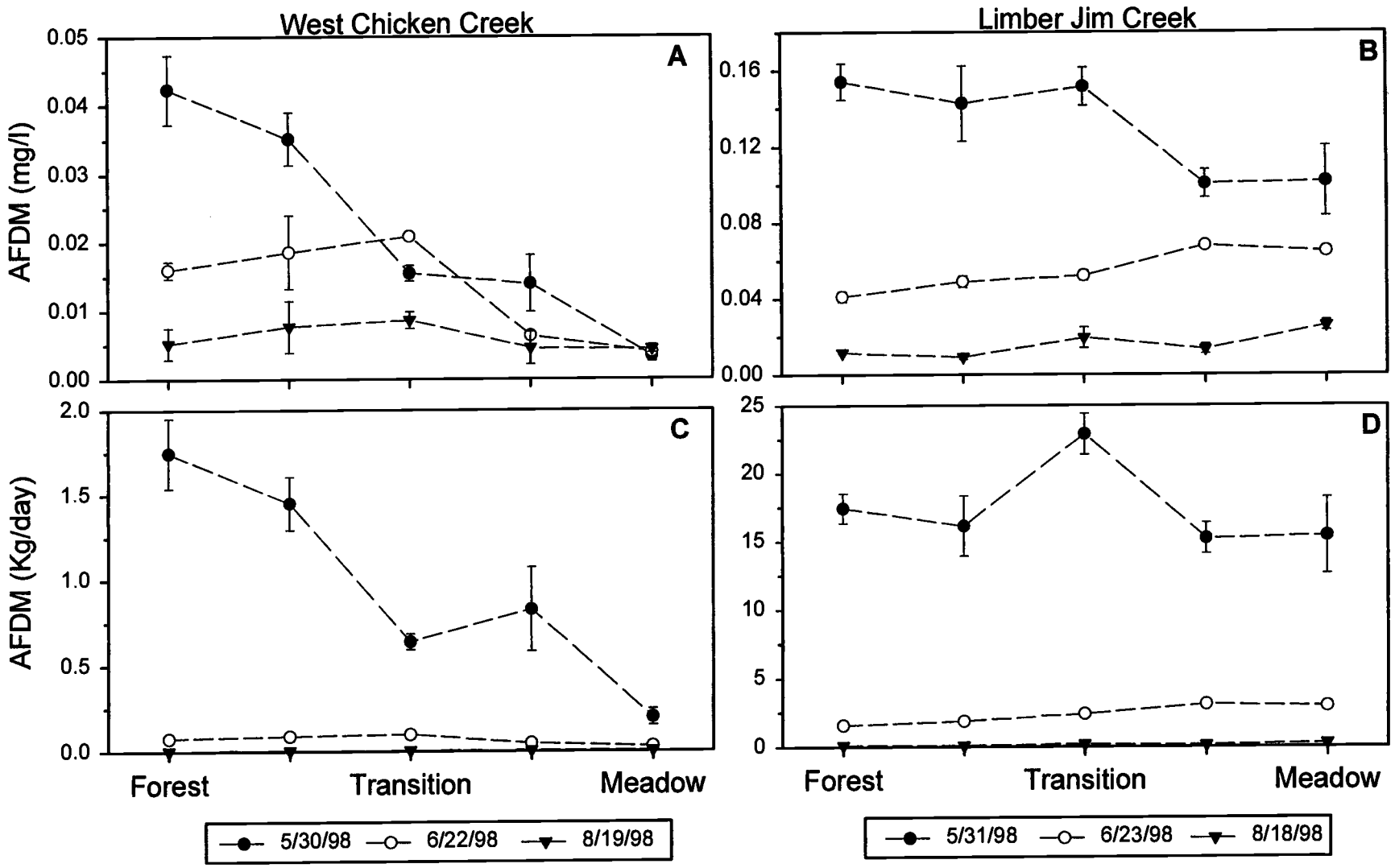

Figure 6. Mean concentration (panels A and B) and transport (panels C and D) of CPOM along the longitudinal gradients in the study streams. Each point is an average ($n = 3$) and vertical bars are one standard error .

during high-flow, concentrations of CPOM were significantly higher ($P<0.0001$ and $P = 0.02$) in the forest reaches than in the meadow reaches of both streams (Fig. 6). Simple linear regressions using all replicate samples indicated that concentration was strongly associated with discharge in the forest reach of West Chicken Creek ($r^2 = 0.78$, $P< 0.0001$, n = 18) and much lower in the meadow reach of West Chicken Creek ($r^2 = < 0.16$, $P = 0.10$, n = 18).

Storage

The mean mass of wood varied considerably between streams and among reaches, ranging from a total of 330 g/ m^2 in the meadow reach of West Chicken Creek to 8,306 g/ m^2 in the forest reach of Limber Jim Creek (Table 6). The mean mass of large and small wood was generally highest in the forest reaches, intermediate in the transition reaches, and lowest in the meadow reaches. Large wood accounted for 84 - 95%, and small wood accounted for 2 - 12%, of total within-channel storage (including CBOM) in all reaches.

CBOM stored within the wetted channel during base-flow in 1999 was highest in the forests, intermediate in transitional reaches, and lowest in the meadows (Fig. 7). In West Chicken Creek, differences in average CBOM among all reaches were significant ($P = 0.048$, Kruskal Wallis test), but not in Limber Jim Creek ($P = 0.19$). In Limber Jim Creek, CBOM in the forest reach was significantly higher ($P = 0.043$) than in downstream reaches when data for transition and meadow reaches were pooled. In all reaches, the majority of CBOM consisted of woody material and needles. In addition, there was a strong positive relationship between the average mass of large wood and the

Table 6. Large and small wood mass (g/ m^2) in study reaches of West Chicken Creek and Limber Jim Creek. Values are averages of three 50m sites per study reach stratified by location within the channels. Active channel values represent wood stored within the active channel but outside of the base-flow stream margins. Numbers in parentheses are one standard error.

Stream	Reach	Size	Wetted width	Active channel	Total
West Chicken Creek	Forest	>10cm	1927.9 (1214.90)	2118.9 (549.1)	2820.8 (968.8)
		<10cm	416.7 (72.6)	199.9 (19.6)	418.2 (39.2)
	Transition	>10cm	1130.5 (192.2)	2741.8 (217.4)	3044.8 (227.5)
		<10cm	262 (56.3)	108.2 (53.0)	178.4 (58.2)
	Meadow	>10cm	78.3 (78.4)	301.8 (214.1)	309.9 (222.1)
		<10cm	100.1 (71.6)	10.4 (10.0)	19.2 (28.1)
Limber Jim Creek	Forest	>10cm	5823.3 (2026.3)	5208.4 (1134.7)	8066.6 (2125.0)
		<10cm	254.3 (39.6)	112.6 (19.6)	239.1 (39.2)
	Transition	>10cm	1390.5 (350.3)	3288.8 (2365.2)	4123.1 (227.5)
		<10cm	127.4 (48.3)	56.3 (27.7)	132.7 (54.8)
	Meadow	>10cm	2146.1 (344.8)	2729.9 (1383.5)	3689.2 (1493.6)
		<10cm	131.7 (62.6)	35.1 (13.7)	93.9 (39.7)

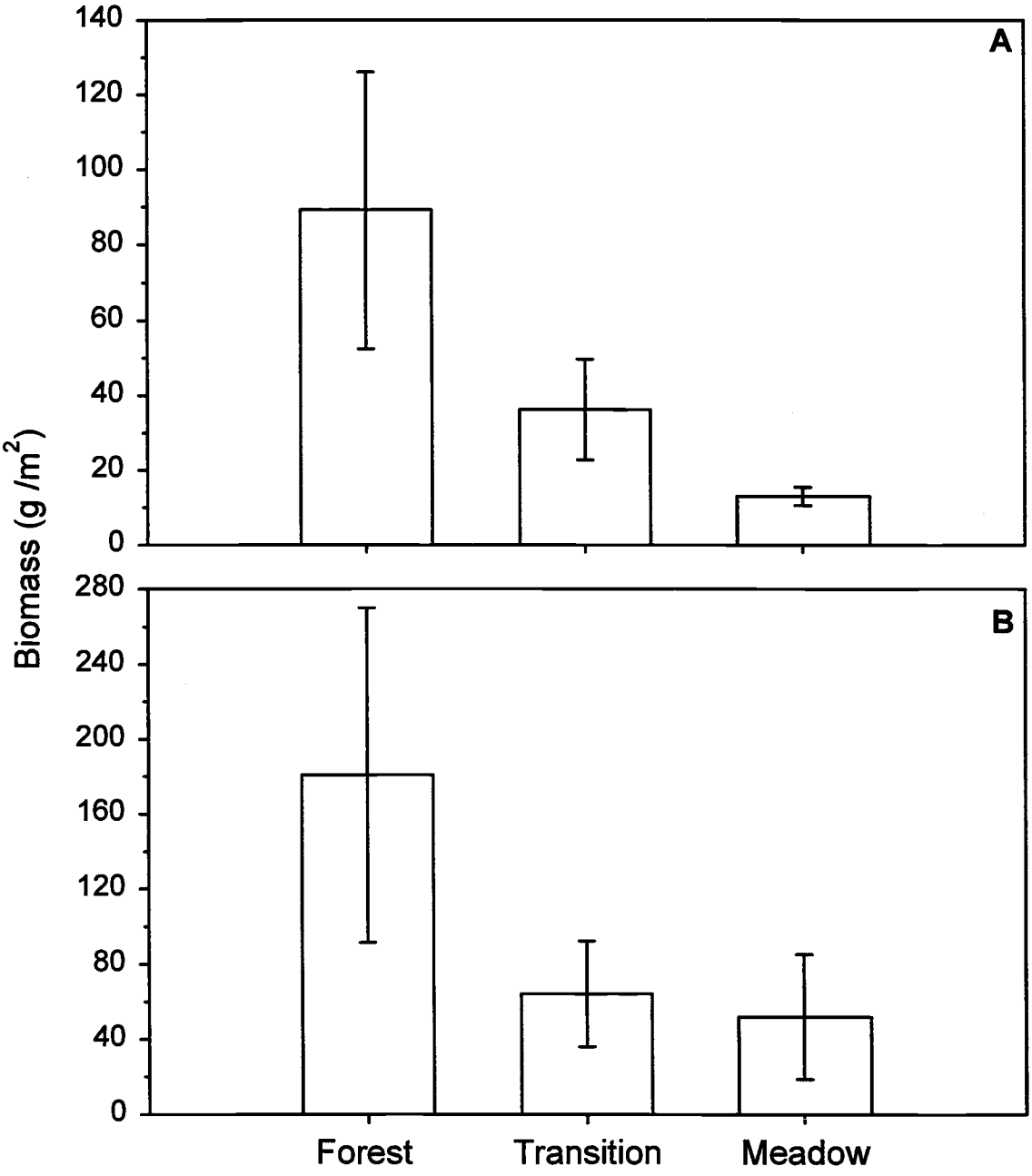

Figure 7. CBOM storage in the study reaches of West Chicken Creek (A) and Limber Jim Creek (B) in fall 1999. Note difference in scale. Bars are averages (n = 10) and error bars represent one standard error.

average mass of CBOM per reach when data from both streams were combined (Fig. 8). The amount of CBOM differed significantly among riffles, pools, and glides at West Chicken Creek ($P = 0.04$) and at Limber Jim Creek ($P = 0.002$) and decreased in the order: pools > riffles > glides. In the forests, pool habitats represented only 30% of units sampled but contained >60% of the total BOM (Appendix D). The quantity of FBOM (>250μm) did not differ among reaches ($P > 0.4$) at either stream (Appendix D).

DISCUSSION

Our results suggest that strong interactions among reach-scale geomorphic characteristics, hydrodynamics, and riparian plant composition produce relatively discrete zones characterized by differences in detritus quality and movement rates. In addition, our results suggest that inclusion of seasonal high-flow organic inputs is critical to understanding energy flow in headwater stream ecosystems where lateral exchange with floodplains occurs. We found that annual CPOM loading was higher in floodplain meadow reaches than in upstream forest reaches. We found no evidence for increased transport rates in the meadows relative to forests during spring high-flow (Fig. 7). Although it is also possible that we overestimated of high-flow inputs and underestimated of high-flow transport rates, it is likely that differences in substrate quality and consequent aquatic decomposition rates and differences in physical CPOM retention among reaches explain this pattern.

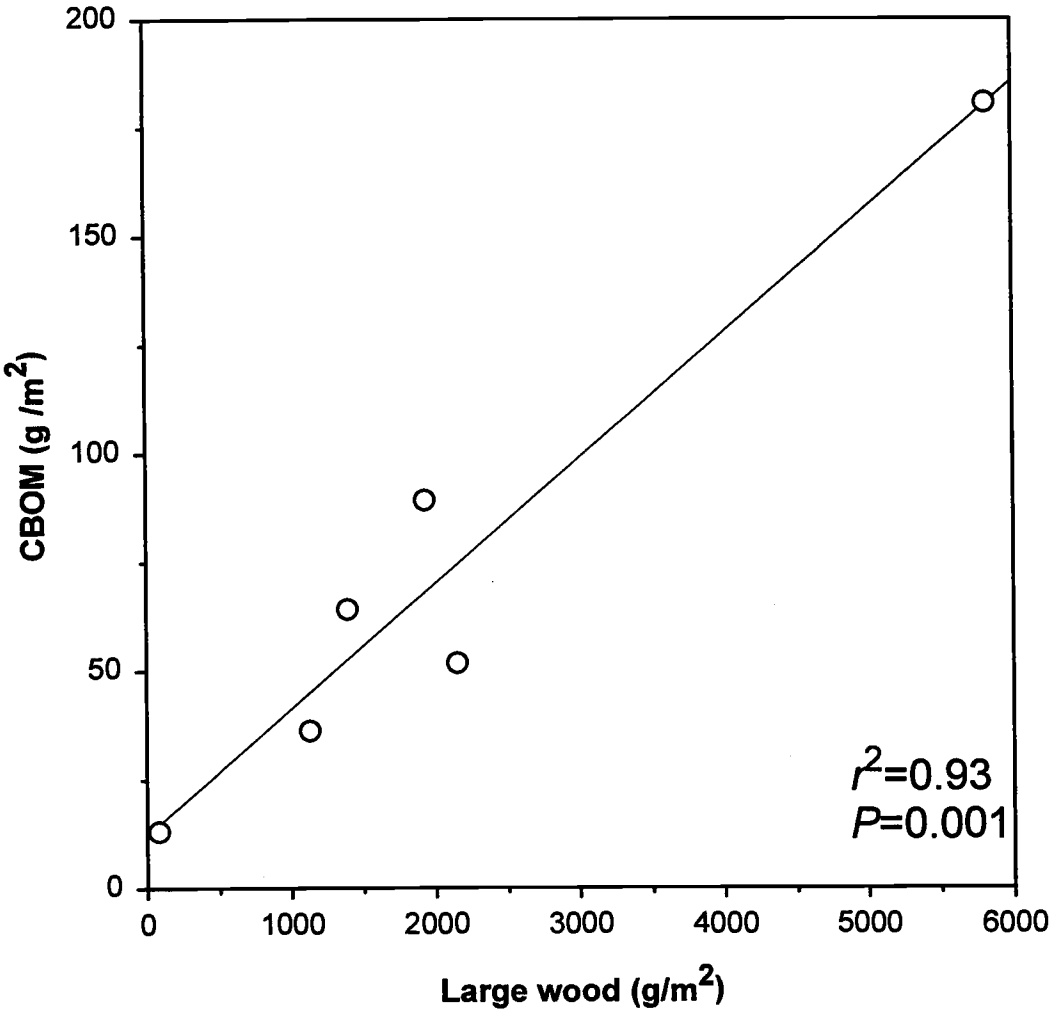

Figure 8. Relationship between large wood mass and CBOM for all reaches in the study streams. CBOM values are averages ($n = 10$) of samlpes collected in 100m sites within forest, transition, and meadow reaches of both streams. Large wood mass was estimated from volumetric inventories of all large wood occurring in the wetted width of the 100m sites.

Detrital import processes

Our estimates of annual fine litterfall inputs to the forests (162 - 173g · m^{-2}·yr^{-1}) were low relative to inputs reported for other coniferous forest headwater streams (213 - 2789g · m^{-2}·yr^{-1}; Minshall et al. 1992, Benfield 1997). Also, estimates of large wood mass within the active channels of our study sites (3-81 Mg/ha) were considerably lower than reported wood mass in small streams draining old-growth coniferous forests in western Oregon (136-300Mg/ha; Lienkaemper and Swanson 1986). These differences are likely due, in part, to the larger tree-biomass of the old growth sites used in these studies. For example, overstory tree biomass in old-growth Douglas-fir forests of the western Oregon Cascade Mountains can be over 800 Mg/ha (Grier and Logan 1977); small streams in these forests receive up to 2789g/m^2 of total litter inputs annually (Sedell et al. 1982). In contrast, overstory tree biomass in the forest reaches of West Chicken Creek and Limber Jim Creek were 149 and 101 Mg/ha, respectively (Case 1995). Although the largest trees were selectively logged in the past, overstory tree biomass was similar to that of other headwater streams in the Upper Grande Ronde basin that have never been logged (125- 177 Mg/ha; Case 1995).

On a stream length basis, our CPOM loading estimates of 271 g · m^{-1}·yr^{-1} and 479 g · m^{-1}·yr^{-1} are similar to those reported for a second-order coniferous stream in Idaho (213- 330 g · m^{-1}·yr^{-1}; Minshall et al. 1992). In our study, lateral movement of detritus in the forest reaches represented <20% of annual litter inputs. These results differ from studies of other coniferous forest streams where steep valley side slopes result in lateral movement accounting for a substantial part of annual inputs (Minshall et al. 1992)

if not much more than litterfall (Sedell et al. 1982). This difference may be attributable to the relatively wide (35-50 m), flat valley bottoms in the study reaches of West Chicken Creek and Limber Jim Creek (Case 1995) that limit direct slope transfer to the streams. By comparison, herbaceous inputs from the active channel during high-flows (Table 3) were similar to annual lateral inputs from the forest floor (~30 g/m^2).

Over the 16 months of litter sampling, the timing and input rates of litter were quite similar between the two forest sites. There were strong seasonal patterns of alder leaf fall and larch needle drop (Fig. 4). Alder leaves have fast decomposition rates and are an important food source for macroinvertebrates (Sedell et al. 1975). In addition, alder leaves accounted for 35 and 70% of annual particulate N inputs to our forest study reaches. Average N input rates from alder leaves during August - October were 13.6 mg $m^{-2} \cdot day^{-1}$ at Limber Jim Creek and 5.6 mg $m^{-2} \cdot day^{-1}$ at West Chicken Creek. Triska et al (1984) found that needles accounted for 49% (0.15 g/ m^2) of litterfall nitrogen inputs to watershed 10 in the H.J. Andrews Experimental Forest and that deciduous leaf input (primarily maple) was only 11% (0.15g/ m^2) of annual inputs. Dominance of *Alnus incana* in the understory of our forest sites resulted in annual broad leaf N inputs of 0.5 and 1.8 g/ m^2.

Over the three years of data collection, the estimated annual input of large trees (diameter >10 cm) to the active channels based upon observed numbers of tree falls within the entire study reaches was 1.6 and 1.3 trees per 500-m reach per year at West Chicken Creek and Limber Jim Creek, respectively. Using an average tree mass of 0.42 Mg/tree calculated from Case (1995), we estimate that whole tree inputs during the study

period were 181 and 328 $g \cdot m^{-2} \cdot yr^{-1}$ at the two sites. Lienkamper and Swanson (1987) found that large wood inputs to headwater streams in western Oregon were highly variable between years, with single trees often accounting for the majority of annual inputs. Whole-tree inputs are often driven by natural disturbance events (Swanson et al. 1998, Bragg 2000), which tend to be patchy over large spatial and temporal scales (Picket and White 1985).

In 1999, a small wind-throw event (~0.30 ha) occurred within the forest reach of West Chicken Creek, which dropped four trees and several tree crowns into a 50-m reach of the stream. We measured all large wood, and counted, measured, and volumetrically sub-sampled (0.008 m^3 samples) all conifer crown piles for AFDM within the active channel of the affected reach. We estimated that this single-day event delivered 7,886 g/m^2 of large wood and 1,721 g/m^2 of branches and needles, for a total of ~ 42 times our estimate of annual inputs. Infrequent, pulse delivery of large trees may determine the abundance and distribution of large wood in small streams (Van Sickle and Gregory 1990), and thereby influence carbon turnover by decaying over long periods of time (Webster and Meyer 1997) and retaining transported organic matter (Bilby and Likens 1980).

Spring flooding was the dominant mechanism of CPOM import to the meadow reaches. Annual inputs to the meadow reaches from litterfall and lateral movement (4 and 14 $g \cdot m^{-2} \cdot yr^{-1}$) were similar to those reported for a northern cool desert stream in Idaho with a sagebrush/grass riparian zone (0.5 to12 $g \cdot m^{-2} \cdot yr^{-1}$; Minshall 1978), but were minor when compared to inputs occurring during ~ three months of spring flooding

(Table 3). While the mechanism for CPOM import differed, estimated annual particulate carbon and nitrogen inputs per m^2 were quite similar between forest and meadow reaches (Table 3). However, because of the large difference in herbaceous biomass (Fig. 5) as well as the greater magnitude of lateral inundation (Table 1), inputs on a stream length basis were 1.6 and 3.8 times higher in the meadows than in forests (Table 2).

We estimated that standing sedge material in the meadow floodplains decreased by >70% during high flows, resulting in fluvial imports of 174 - 445 g AFDM $\cdot$ $m^{-2} \cdot yr^{-1}$ to the meadow reaches (Table 3). Although our pre-flood standing crops of 400 and 645 g/m^2 are probably underestimates of annual production, these values are similar to estimates of aboveground production in a wide range of temperate *Carex* wetlands (550 - 800g $\cdot$ $m^{-2} \cdot yr^{-1}$; Bernard et al. 1988). Assuming that much of unattached *Carex* litter in the fall was current-year production (Gorham and Somers 1973), our results suggest that much of primary production in these near stream sedge communities may be incorporated into the streams on an annual basis.

Rhizomatous sedges translocate much of their aboveground photosynthates to root systems at the end of the growing season (Gorham and Somers 1973, Bernard et al. 1988). While pre-flood biomass sampling occurred at the end of the growing season after the occurrence of several frosts, further belowground transport likely occurred. The *pre-*flood litter AFDM, carbon, and nitrogen concentrations (Table 4) probably reflect both potential belowground translocation and terrestrial leaching losses and therefore produce conservative estimates of particulate C and N inputs (Table 3). Our application of a 10% mass loss seems reasonable based upon the decreases in carbon concentrations (5.7 –

8.7%) and percent AFDM (7.4 - 24%) from pre-*standing* material to pre-*litter*. Decreases in *post*-flood litter AFDM were greater (13.1 – 28.8%; Table 4), but in addition to further leaching losses incurred during flooding, these values also reflect flood-deposited inorganic sediments that were not removed during laboratory rinsing. In addition, our methods did not account for burial of plant material by sediments; although there were zones of sediment aggradation in both meadow reaches (*personal observation*), we do not know the influence of burial on the flux of aboveground plant biomass.

Because microbial activity typically increases during periods of snow-melt (Brooks et al. 1998), the majority of decomposition may have occurred during early spring as temperatures increased and snow on the meadows melted. It seems unlikely that winter decomposition of sedges at our sites would have been substantially higher than the average literature value ($k = 0.5$) calculated from field studies that spanned at least part of a growing season (Verhoeven and Arts 1987, Aerts and De Caluwe 1997, Thorman and Bayley 1997, Arp et al. 1999). Temperature increased in near-stream wells and water table elevation began to rise and shallowly inundate near-stream sedge communities in April (Dwire, *in progress*), one month before peak flows. Thus, particulate fragmentation losses occurring during this period would be considered allochthonous input. Moreover, tissues that were fragmented into FPOM in the fall or winter may have ultimately been entrained during the early rise in discharge.

Floodplain areas may behave as detrital sources or sinks depending on hydrodynamics, topography, and sediment loading (Cuffney 1988). Our paired-plot design allowed us to estimate flux of *total* aboveground material, and thus account for depositional processes. We found a net decrease in herbaceous biomass from fall to

spring at both forest and meadow sites (Fig. 5). The *average* mass of unattached dead graminoid litter did not differ between *pre-* and *post*-flood samples, yet several plots in both of the meadows had considerably more litter after spring flooding than before (up to six times more), thus showing the high spatial variability in accumulation *versus* loss among plots. Results of experimental leaf releases conducted in meadow reaches of West Chicken Creek indicated that much of the CPOM initially retained within the channel during high-flow was transported further downstream and eventually captured on the floodplain in vegetated side channels and at meander bends during the falling limb of the hydrograph (Chapter 3). Although CPOM accumulation was observed on the meadow floodplain of Limber Jim Creek, higher stream power and a larger channel resulted in much higher downstream transport (Chapter 3).

Longitudinal patterns of transport and storage

Based upon our estimates of organic matter inputs to the meadow reaches during spring high-flow, we expected concomitant increases in CPOM concentrations in the water column. It is likely that our high-flow drift samples underestimated transport rates occurring during spring flooding because we did not sample drift during the rising limb of the hydrographs. Seston concentrations during high flows are generally higher on the rising limb than on the falling limb of the hydrograph, due to rapid increases in discharge and entrainment of material as areas within the active channel become exposed to currents (Bilby and Likens 1979, Webster et al. 1987). High flows generally transport a disproportionate amount of the annual seston load in small streams (Fisher and Likens

1973). Discrete sampling can dramatically underestimate peaks in concentration during increases in discharge and therefore underestimate annual transport (Cuffney and Wallace 1988).

It is likely that we simply missed the pulse in transport in the meadows because of very low sampling intensity. Moreover, the high percentage of the variation in CPOM transport explained by discharge in both forests and all sites in Limber Jim Creek (77-95%) as well as the low variation explained in the meadow of West Chicken Creek (16%), are probably artifacts of very low sampling intensity ($n = 3$ flow levels per stream). Even the most accurate rating curves (CPOM concentration vs. discharge) developed from continuous total sampling of stream flow, typically explain less than 50% of CPOM concentration (Cummins 1983). However, high flow samples were taken very near to peak flow discharge in both streams (30 and 31 May 1998; Appendix A). Therefore, assuming that much of the CPOM immediately available for transport was exported during the rising limb (Appendix A), the higher concentrations in the forests (Fig. 6) suggest higher overall availability of CPOM for transport.

This observation is consistent with downstream decreases in CBOM storage (Fig. 7). In addition, experimental leaf releases conducted during high flow indicated that the forest reaches were much more retentive of CPOM than meadow reaches of both streams (Chapter 2). During high flow, seston concentration in the forest reaches was 0.10 mg/l in Limber Jim Creek and 0.038 mg/l in West Chicken Creek, yet the ratio of concentration to discharge at both site was ~ 0.04, suggesting that higher transport rates in Limber Jim Creek are a function of stream size. Differences between the two streams in CBOM, large wood, and detrital loading are proportional to differences in stream size

as well. Given our estimates of higher detrital loading in the meadow reaches (Table 2), the apparent higher availability of CPOM for transport in the forest reaches is probably influenced by a larger source area of forest-derived CPOM. Specifically, the length of forested stream upstream of the forest reaches (2 – 3 km) is much longer than the length of stream dominated by meadow vegetation upstream of the meadow reaches (0.5 – 1.5 km; Fig. 1). The importance of CPOM source size can be illustrated by comparing differences in loading rates and CBOM between the two forest reaches. Although total annual inputs per stream surface (Table 2) and mean C:N ratios of inputs (Table 3) were higher in the forest reach of West Chicken Creek, CBOM storage was much higher in Limber Jim Creek (Fig. 7) despite being much less physically retentive (Chapter 3).

Channel morphology of the two streams may partly explain differences in longitudinal patterns of transport during high flow: the stream channel of Limber Jim Creek is much wider and deeper than that of West Chicken Creek. Consequently, the average width of bank inundation in the meadows during spring flooding was lower in Limber Jim Creek (3.4 m) than at West Chicken Creek (10.7 m), despite discharge being >2.5 times higher in Limber Jim Creek. Thus, concentration of hydraulic energy in Limber Jim Creek results in a more conduit-like channel than in West Chicken Creek where extensive over-bank flow and decreased velocity allows for more settling out and deposition of particles.

The rate of downstream movement (v) of POC may be used as an estimate of reach level physical carbon spiraling (transport and retention)(Newbold et al. 1981,1982, Minshall et al 1983). It is calculated by dividing the daily flux of transported material (g/day) by the product of BOM (g/m^2) and mean stream width (m). Using base flow

estimates of transported and stored CPOM, calculated rates of downstream movement along the two streams were 0.03, 0.11, and 0.31 m/day at West Chicken Creek, and 0.18, 0.86, and 1.36 m/day at Limber Jim Creek, in forest, transition, and meadow reaches, respectively. In contrast, using the same values of BOM to estimate v during high-flow produced estimates of 10.9, 10.8, and 24 m/day at West Chicken Creek and 31, 97.4, and 97.5 m/day at Limber Jim Creek. These longitudinal trends are corroborated by the empirical results of leaf releases conducted to estimate CPOM retention (Chapter 3).

Greater availability of CPOM for transport in the forest reaches is likely also due to different decomposition rates of dominant plant tissues. CBOM stored in the forest reaches in fall 1999 was an average of 88 g/m^2 at West Chicken Creek and 177 g/m^2. These values are similar to those reported for other coniferous forest headwater streams in the PNW (Speaker 1985, Minshall et al. 1992). In contrast, CBOM storage in transitional and meadow reaches was 2.5 - 6.8 times lower than that in the forest reaches (Fig. 7). Graminoids generally decompose more slowly than other herbaceous plants but much faster than conifer needles and woody material (Webster and Benfield 1986). This is primarily due to differences in chemical quality; tissues with high C:N ratios and lignin concentrations decompose slowly (Enriquez et al 1993). Lignin concentrations of sedges are generally <7% (Aerts et al. 1997), whereas lignin concentrations in needles and woody material range from 24 - 50% (Triska et al. 1975, Melillo et al. 1983). In addition, lignin: N ratios of *Picea engellmanii* foliage range from 35 –55 whereas lignin: N ratios of graminoids are generally < 8 (Scott and Binkley 1997). Moreover, C:N ratios of needles and CTBW in litterfall at the forest sites in our study ranged from 41 - 104, while C:N ratios of sedge blades ranged from 21 - 57. Despite significant differences between

forest and meadow C: N ratios (Table 5), weighted C:N ratios of total annual inputs were similar between forest and meadow reaches (35 – 50; Table 3). However, this narrow range was driven by only three months of high N alder leaf inputs in the forest reaches.

Our estimates of CBOM in the meadows (13 and 52 g/m^2) are higher than that reported by Scarsbrook and Townsend (1994) for tussock grassland streams in New Zealand (0.17 - 6.53 g/m^2) but much lower than that reported by Gurtz et al. (1988) for an ephemeral prairie stream in Kansas (291 - 341 g/m^2). Because CBOM was sampled in late September, any coarse sedge material reflected what remained after ~ 4 months of in-stream decomposition as well as minor summer lateral inputs. Large and small wood occurred at all sites but was minor in the meadow reach of West Chicken Creek. In contrast, the abundance of large and small wood in the transition and meadow reaches of Limber Jim Creek was relatively high. Here, the majority of existing wood in the channel was installed by the USFS to improve fisheries habitat. Indeed, 87% of CBOM stored in the meadow reach of Limber Jim Creek was woody material in pools associated with debris jams. This observation, together with the strong association between large wood and CBOM storage among reaches (Fig. 8), reflects both the capacity of wood to retain finer CPOM (Bilby and Likens 1980) as well as the increased likelihood that reaches with higher inputs of CTBW also have higher inputs of large wood, the two of which may occur together (i.e., during wind-throw events).

The residence time of CPOM can be estimated by calculating turnover time (BOM / total input rate), a metric which expresses the period of time (years) required for complete replacement of CBOM (Webster and Meyer 1997). Using our fall CBOM values (Fig. 7) as an estimate of annual storage and total inputs (litterfall, lateral, and

high-flow), calculated turnover times were 0.42 y and 0.97 y in the forest reaches and 0.05 y and 0.24 y in the meadow reaches of West Chicken Creek and Limber Jim Creek, respectively. These estimates are consistent with higher physical retention rates (Chapter 3) and presumed slower decomposition rates in the forest reaches compared to the meadow reaches. When high-flow herbaceous inputs were excluded from the calculation, turnover times increased to 0.55 y and 1.22 y in the forest reaches and to 3.26 y and 1.29 y in the meadow reaches. These values clearly do not account for our finding that 81 – 98% of annual CPOM input to the meadow reaches was herbaceous material. This suggests that exclusion of pulsed floodplain inputs, particularly of labile herbaceous material, may dramatically overestimate turnover times in stream ecosystems. Also, by including estimates of whole tree inputs (see *Detrital Import Processes*) and wood storage within the wetted width of the stream channels (Table 6), calculated turnover times in the forest reaches were orders of magnitude longer (13.3 y and 19.5 y) than in the meadow reaches.

Calculations of turnover times typically only include organic matter stored within the wetted width of the stream channel (Webster and Meyer 1997) and ignore organic matter on adjacent floodplains. In our study, the mass of post-flood litter remaining on the stream banks in the meadow reaches (200 and 114 g/m^2) was much higher than the litter mass remaining on the banks of the forest reaches (13 and 14 g/m^2; not including wood)(Fig. 5). The large quantity of litter remaining in the active channel in the meadow reaches was likely the combined result of deposition during the falling limb of the hydrograph (Chapter 3) and resistance of attached sedge blades to entrainment during high-flow. Considering the floodplain as part of the wetted width of the stream during

high-flow, we calculated turnover times for floodplain litter mass. In contrast to longer turnover times of CBOM in the forest reaches, calculated floodplain litter turnover times were 0.06 y and 0.08 y in the forest reaches and 0.75 y and 0.53 y in the meadow reaches of West Chicken Creek and Limber Jim Creek, respectively. These estimates do not account for terrestrial decomposition occurring between spring high-flow events and are, therefore, probably overestimates of turnover time. However, they do suggest that complete turnover of floodplain litter may occur within one flood cycle in the forests but may take multiple years in the meadows. Together, with our estimates of higher CPOM loading in the meadow reaches, these calculations suggest that inclusion of spatial and temporal dynamics of detritus in herbaceous floodplains should be explicitly considered in the development of organic matter budgets of headwater ecosystems

Organic matter dynamics and riparian patchiness

A critical contribution to stream and riparian ecology has been the recognition that interactions among landforms, geomorphic processes, and organisms shape ecosystem patterns and processes over various temporal and spatial scales (Vannote et al. 1980, Swanson et al. 1988). Landform features and associated disturbance regimes strongly influence the distribution, composition, and structure of riparian zones and energy and nutrient flow within them (Swanson et al. 1988, Gregory et al. 1991, Montgomery 1999). In this study, we found downstream shifts in detrital dynamics consistent with changes in topography and dominant riparian vegetation, specifically downstream shifts to low-gradient alluvial-floodplain geomorphology and concomitant change in riparian plant

composition, resulting in a downstream increase in the importance of pulsed CPOM entrainment during seasonal flooding. By contrast, the frequency of periodic pulse inputs of coniferous trees during wind-throw events was much higher in the forest reaches. In turn, these pulse inputs of wood and other recalcitrant material likely slow the turnover time of organic matter through enhanced retention (Chapter 3) and low decomposition rates.

Riparian soils in the floodplain meadow reaches are composed of alluvial silts and clays (Dwire 2000). It is likely that much of the soil composing the stream banks and influencing channel morphology in the meadow reaches is ancient volcanic ash delivered via fluvial transport from upstream and adjacent uplands (Harward and Youngberg 1970). Graminoid plants, particularly *Carex*, generally dominate plant communities on fine-textured sediments in meadow floodplains of the Upper Grande Ronde Basin (Crowe and Clausnitzer 1997). Thus, distant volcanism and sediment transport may have produced the floodplain landforms present today, thereby influencing longitudinal patterns of energy and material flow in headwater stream ecosystems of the region.

Of particular significance in our study was the quantification of floodplain particulate inputs, a frequently missing component of stream organic matter budgets (Webster and Meyer 1997). In our study, we have demonstrated that up to 98% of annual inputs of detritus to meadow stream reaches were derived from adjacent herbaceous-dominated floodplains. Even in the forest reaches, where the majority of inputs were from litterfall and lateral movement, over 20% of annual input was of herbaceous material captured during spring high-flow. While the magnitude of high-flow inputs will

clearly vary from year to year depending upon flow conditions, our study underscores the importance of estimating of pulse organic matter inputs.

The landscape position of the meadows may ultimately determine any influence on larger scale longitudinal ecosystem patterns. In West Chicken Creek and Limber Jim Creek, the meadow reaches occur at the topographical and vegetative beginning of the large, open floodplain meadow system of the main-stem Grande Ronde River. Had the longitudinal position of the meadows been reversed (meadows upstream of forests), we likely would have observed different patterns. In this light, our finding of dramatic differences in detrital dynamics over relatively small spatial scales emphasizes the importance of spatial heterogeneity in hydro-geomorphic characteristics and riparian plant composition to our understanding of the structure and function of headwater stream ecosystems.

Most research in stream ecology focuses on single, small stream reaches characterized by relatively homogenous vegetation. Indeed, the major conceptual model of headwater streams in lotic ecology is that of a linear, uniformly closed-canopy, small tributary with high levels of deciduous leaf inputs (Minshall et al. 1992, Fisher 1997). Had we only studied reaches within forests or meadows exclusively, generalizations to the entire streams would have been erroneous. If our conceptual frameworks of energy and material flow in stream and riparian ecology are to become more general in their applicability, research must explicitly address reach and valley-segment scale patchiness in structure and processes within the headwaters. Moreover, management strategies must recognize that spatial and temporal heterogeneity in stream and riparian ecosystems is biologically meaningful. In northeast Oregon, this ecological variation in the landscape

was part of the historical habitat template for now-endangered salmon and steelhead populations. Better understanding and management of these ecosystems is essential to maintaining and restoring biodiversity.

CHAPTER 3

Influences of Seasonal Flooding, Geomorphology, and Riparian Vegetation on Organic Matter Retention in Two Headwater Streams

E.N. Jack Brookshire

Influences of Seasonal Flooding, Geomorphology, and Riparian Vegetation on Organic Matter Retention in Two Headwater Streams

ABSTRACT

Retention of coarse particulate organic matter (CPOM) was investigated in two headwater tributaries of the Upper Grande Ronde River in northeast Oregon. CPOM retention was estimated by introducing tracer leaves into the stream channels along short-scale longitudinal gradients from constrained forest reaches to unconstrained floodplain meadow reaches. Leaves were released at nine sites during summer base-flow and four sites during spring high-flow. Retention rates were calculated with a negative exponential decay model. Average travel distances of leaves ranged from 0.9 to 97m for all releases and were significantly longer during high flow than during base-flow in all reaches. During high-flow, the forest reaches were significantly more retentive of CPOM than meadow reaches. Retention in the forests was largely associated with the stems of riparian shrubs and accumulations of stream wood. In contrast, retention in the meadows occurred more on streamside herbaceous vegetation and in backwaters. In the meadows, complex patterns of CPOM movement from the stream channel to the floodplain occurred in the meadows resulting in long-term retention. However, the degree of lateral exchange was dependent on channel morphology and riparian vegetation structure. Despite large variation among reaches in riparian vegetation, channel characteristics, and large wood abundance, hydro-geomorphic variables (thalweg depth and stream width) explained the most variation in retention among all reaches. Results of this study suggest that reach

and valley-segment scale variation in dominant riparian vegetation and hydro-geomorphic characteristics strongly influence spatial and temporal patterns of detrital movement in headwater streams.

INTRODUCTION

Headwater streams draining forest ecosystems retain much of the detrital organic matter entering from adjacent riparian zones (Bilby 1981, Minshall et al. 1983, Speaker et al. 1984). Allochthonous coarse particulate organic matter (CPOM: >1mm in size) constitutes a large proportion of fixed carbon in small, forested streams (Cummins 1974). However, because material is largely transported downstream, most microbial and invertebrate utilization of CPOM depends upon it being physically trapped and stored within the channel (Lamberti and Gregory 1996). Complex channel morphology (Speaker et. al. 1984), accumulations of wood (Bilby and Likens 1980), and riparian vegetation (Speaker et al. 1988) interact to retain CPOM. Subsequent to retention, CPOM undergoes leaching, physical fragmentation, and a sequence of biological processing (Webster and Benfield 1986). Consequently, organic export from small streams is dominated by fine and dissolved organic matter (Bormann et al 1969, Fisher and Likens 1973, Minshall et al. 1983, Webster et al. 1990, Wallace et al. 1991).

Studies of longitudinal patterns in carbon dynamics have found that CPOM retention generally decreases as stream order increases (Minshall et al. 1983, 1992; Naiman et al. 1987). This observation is based largely on indices of reach-level carbon spiraling derived from relationships among organic inputs, storage, transport, and

community respiration (Fisher 1977, Newbold et al. 1982, Elwood et al. 1983). However, because organic matter inputs and outputs can be highly variable among years (Cummins et al. 1983), indirect measures of retention may not adequately assess the physical capacity of a stream to trap and store material without accompanying long-term data on these parameters (Wallace et al. 1995). Alternatively, retention can be estimated empirically by releasing known quantities of particles into a stream reach and expressing retention as the percent of the particles released that are still in transport at a given distance downstream (Young et al. 1978, Speaker et al. 1984).

Leaf release studies conducted in a wide variety of small forested streams around the world have consistently found that average travel distances of leaves are quite short, generally being <50m but up to 200 m in length (Young et al. 1978, Speaker et al. 1984, Speaker et al 1988, Jones and Smock 1991, Petersen and Petersen 1991, Prochazka et al. 1991, Snaddon et al. 1992, Wallace et al. 1995, Ehrman and Lamberti 1992, Webster et al. 1994, Raikow et al. 1995). Moreover, releases of dowels to estimate small wood retention typically yield even shorter travel distances than leaves (Jones and Smock 1991, Wallace et al 1995).

Most CPOM export in small streams occurs during periods of high discharge (Fisher and Likens 1973). Therefore, conducting releases only during periods of base flow will likely not adequately estimate annual movement of CPOM, particularly export to downstream reaches. Several studies have reported increased travel distances during periods of high discharge (Speaker 1985, Webster et al. 1987, Jones and Smock 1991, Snaddon et al. 1992, Scarsbrook and Townsend 1994, Wallace et al. 1995). But,

retention by riparian vegetation (Speaker et al. 1988) and on floodplains (Jones and Smock 1991) may also increase during seasonal flooding.

Despite considerable emphasis on conceptualizing streams as mosaics of different reaches or valley segments with distinct geomorphic, fluvial, and riparian characteristics (Swanson et al. 1988, Pringle et al. 1988, Gregory et al. 1991, Townsend et al. 1996, Montgomery 1999), little is known about CPOM retention in streams with natural non-forested riparian zones (e.g., meadows, grasslands). Previous studies in grassland streams have suggested that processes of CPOM retention in streams with open, herbaceous riparian zone likely differ from dominant retention processes in forested streams due to channel characteristics and a lack of large wood (Gurtz et al. 1988, Scarsbrook and Townsend 1994).

In Chapter 1 we found that benthic storage and transport concentrations of CPOM were significantly higher in upstream forest reaches than in downstream meadow reaches of West Chicken Creek and Limber Jim Creek. There was a strong association between in-channel large wood and coarse benthic organic matter (CBOM) among reaches, suggesting that wood has an important role in CPOM retention in these streams. In addition, the rate of downstream movement of CPOM (v, in meters per day), was estimated to increase longitudinally from forest to meadow reaches during summer base-flow and during spring high-flow. However, annual CPOM loading was higher in the meadows due to import of herbaceous biomass during spring flooding. These lines of evidence suggest a longitudinal decrease in the retentive capacity of the two streams.

Our objectives were to investigate spatial and temporal patterns of CPOM retention in the two study streams by conducting releases of tracer particles. We were

interested in longitudinal patterns (forest to meadow) in retention as well as differences in retention between high and low flow periods. We hypothesized that in-channel retention would be higher in the forest reaches than in the meadow reaches. We also expected that differences in riparian characteristics, channel morphology, and flood hydrodynamics would result in different mechanisms of retention such as debris dams *versus* floodplain deposition between forest and meadow reaches.

METHODS

Study sites

The study sites are located along West Chicken Creek (45°3'17"N, 118°24'11"W) and Limber Jim Creek (45°06'15"N, 118°19'41"W), both second-order tributaries to the Upper Grande Ronde River in the Blue Mountains of northeastern Oregon (Fig. 1). Mean annual precipitation is 540 mm, the majority of which occurs as snowfall from November to May (PNW Research laboratory, La Grande, Oregon). Spring snowmelt produces the peak discharge in the hydrographs of these streams, which occurs between April and June (USFS, La Grande)(Appendix A). Limber Jim Creek has a larger drainage area and higher discharge than West Chicken Creek, but the two are similar in elevation, gradient, and canopy cover (Table 1).

Both streams flow through a coniferous forest section into an open meadow section before their confluence with the Upper Grande Ronde River. We selected three study reaches distributed along the longitudinal gradient of each stream: 1) a 500-m reach

within the upstream forest; 2) a 500-m transition reach located between the forest and meadow reaches; and 3) a 250-m reach in the downstream meadow section (Fig. 1). Valley width increases downstream in both streams and channel morphology generally becomes less constrained downstream. Dominant channel substrates are gravels and cobbles at all sites. A tributary entering West Chicken Creek downstream of the transition reach contributes 30 - 40% of mainstem discharge to the meadow throughout the year. Likewise, a tributary entering Limber Jim Creek upstream of the transition reach contributes 5 - 26% of mainstem discharge.

Overstory vegetation at the forest sites is composed of several coniferous tree species, primarily Engelmann spruce (*Picea engelmanii*). Mountain alder (*Alnus incana*) occurs almost continuously along the stream edge of Limber Jim Creek but is distributed in small clumps along West Chicken Creek (Case 1995). Large and small wood is abundant in the stream channels in the forest sections and decreases in abundance longitudinally in both streams (Chapter 2). However, a considerable amount of large wood has been placed in the channel of the meadow section in Limber Jim Creek by the USFS to improve fisheries habitat. Dominant vegetation in the meadow sites consists largely of graminoid plants (sedges and grasses)(Dwire 2000). Tree canopy cover is low in the meadows (<5%)(Chapter 2, Table 1) but scattered patches of conifers (primarily *Pinus contorta*) occur, and at Limber Jim Creek alder and willow (*Salix* spp.) are common. Riparian plant composition occurring between the downstream end of the forest reaches and the upstream end of the meadow reaches is compositionally transitional, consisting of a patchy *P. contorta* and alder overstory with an herbaceous, largely graminoid, understory.

During a period of spring high discharge (Appendix A) we selected two 50-m (valley length) sites within each larger forest and meadow study reach into which we released particles, for a total of four release sites per stream. Stream lengths of sites ranged from 63-113 m depending upon sinuosity (Appendix B). Sites were selected to encompass a wide range of channel features and variation in riparian vegetation representative of the forest and meadow reaches. During a period of summer base flow (Appendix A) we randomly selected three 50-m (stream length) sites within the larger study reaches in locations overlapping spring sites and within the transition reach, for a total of nine release sites per stream.

Leaf releases

We estimated short-term CPOM retention by releasing batches of abscised *Ginkgo biloba* leaves (n = 1000/ release) into the study streams during a period of spring flooding and summer base-flow. We also wanted to investigate the retention of graminoid leaf blades because graminoid plants, particularly sedges, constitute the majority of detrital biomass incorporated into the meadow reaches during spring high-flow (Chapter 1). To do this, we conducted releases of waterproof paper ("Rite in the Rain", J.L. Darling Corporation, Tacoma, Washington; Webster et al. 1994) cut into ~ 1 x 28 cm strips (n = 770/ release) during a period of high discharge. This material was chosen because it could be cut into the approximate shape of sedge blades and because the white color allowed for easy detection within the channel.

Ginkgo leaves were used as a CPOM tracer in all study reaches in order to compare among reaches. We did not independently compare paper strips to sedge blades or *Ginkgo* leaves to alder leaves, needles, and wood, and therefore cannot estimate actual retention rates of naturally occurring CPOM. However, we have no reason to expect that relative patterns in retention among reaches would have differed had we used different CPOM tracer types.

Before release, all particles were soaked in water for 12 hours to impart neutral buoyancy (Speaker et al. 1984). Released particles were distributed evenly across the width of the channel. In the meadows, paper strips were released shortly after *Ginkgo* leaves. Non-retained leaves were caught at the downstream end of the reach with a seine net staked to the channel-bottom and stretched across the wetted width of the channel. Two to three hours after the leaves were released, we collected and counted leaves captured in the net. We then surveyed the site by visually estimating the number of leaves within 1m increments downstream of the release point and noting the dominant retention feature.

To investigate factors that might affect leaf retention within a reach, we estimated large and small wood volumes (described in Chapter 1), and noted the number of debris dams. Stream width measurements ($n > 50$) were taken within each 50 m release site. Discharge was monitored at the downstream end of the meadow reach of both streams by the USFS La Grande District during the study period. We estimated discharge in the forest reaches at three locations using a flow meter (Swoffer 2100). Thalweg depth and velocity were measured at 5 -10 locations in each forest, transition, and meadow site during high- and low-flow releases.

In July 1998, after high-flow waters had completely receded, we estimated the retention of strips on the meadow floodplains by measuring the distance (perpendicular to stream flow) between the stream edge and the nearest edge of each deposited strip (n = 415 at West Chicken Creek and n = 76 at Limber Jim Creek). To illustrate spatial patterns of floodplain retention, the distribution of deposited strips was overlaid onto detailed maps of floodplain sections where the majority of deposition occurred.

Data analysis

The percent of total leaves released that were caught in the net was fit to a negative exponential decay model (Young et al. 1978):

$$T_d = T_0 e^{-kd}$$

where T_d is the percent of total released particles in transport at distance d (m) from the release point, T_0 is 100%, and k is the instantaneous retention rate. Visual inventories did not yield the total number of leaves released. Therefore, data was normalized to the percentage of leaves found (Speaker et al. 1984). Because turbidity during high flow releases greatly reduced our ability to positively identify leaves within the channel, we based our calculation of slope ($-k$) on two data points, T_0 and T_d (Lamberti and Gregory 1996). The average travel distance (m) of particles is the inverse of the retention rate (1/k) (Young et. al 1978, Newbold et al. 1981). For all but one release conducted during low-flow at West Chicken Creek, all *Ginkgo* leaves were retained well upstream of the net. To calculate retention rates for these sites, we considered the maximum downstream location of *Ginkgo* leaf travel = d and then added one particle to the calculation of T_d,

thus making it equal to 0.1% in transport at d_{max}. Therefore, to compare among sites we added 0.1% to the T_d of every release.

We plotted the longitudinal distributions of leaves in transport estimated from visual surveys of release sites (retention curves) and curves generated by the negative exponential decay model. We then determined the amount of variation in the survey data explained by the model using simple linear regression. Travel distances for all sites within each reach (forest, transition, and meadow) and for base- and high-flow releases were averaged and compared using t-tests. Multiple linear regression analysis using backward elimination of non-significant ($P>0.05$) explanatory variables (SAS, version 6.12, SAS Institute Incorporated, Cary, North Carolina, USA; Ramsey and Schafer 1997) was applied to retention data to determine which combinations of parameters best explained average travel distances for all releases in both streams. Variables included in the analysis were stream, reach, site, discharge, thalweg velocity, stream width, thalweg depth, large and small wood volume, and number of debris dams. Travel distances were then regressed against the most significant explanatory variables using simple linear regression.

RESULTS

Variation in hydrology, geomorphology, and riparian plant structure strongly influenced leaf retention in West Chicken Creek and Limber Jim Creek. During spring high-flows, the forest reaches were significantly more retentive of CPOM than downstream meadow reaches. Average travel distances in the forests were less than half the length of travel distances in the meadows (Table 7). Retention was much higher

during base-flow than during high-flow in all reaches; average travel distances during base-flow were 14.6 times shorter in West Chicken Creek and 2.6 times shorter in Limber Jim Creek (Fig. 9). These patterns are likely due to inter-stream and seasonal differences in discharge, differences in large and small wood abundance, geomorphic characteristics of the stream channels, and the type of near-stream riparian vegetation.

There was considerable variation in retention rates among sites and between streams: average travel distances of *Ginkgo* leaves ranged from 0.9 m to 97 m for all releases conducted in both streams. For most of the base flow releases, observed patterns of leaf retention fit the negative exponential model well, with 8 out of 9 releases at Limber Jim Creek with r^2's ≥ 0.85. Observed data did not conform as well to the model in West Chicken Creek, with 2 of the 9 releases having r^2's < 0.28 and a stream average $r^2 = 0.68$. However, in both streams, major divergence from model predictions were explainable by the presence of debris dams and other retentive features which captured the majority of leaves in transport. During high-flow, 5 out of 6 releases in West Chciken Creek and 4 out of 6 releases in Limber Jim Creek had r^2's ≥ 0.82 (Appendix B).

Seasonal differences in retention

During high-flow, average travel distances were significantly longer in the meadows than in the forests in West Chicken Creek ($P = 0.015$) and in Limber Jim Creek ($P = 0.057$)(Table 7, Fig. 9). Average travel distances ranged from 20 – 36 m in the forests and from 49 – 97 m in the meadows. Travel distances in Limber Jim Creek were consistently higher than those in West Chicken Creek for all releases except for paper

strips (Table 7, Fig. 9). Average travel distances of paper strips during high flow were an average of 41.9 and 24.5 m versus *Ginkgo* travel distances of 63.4 and 74.6 m in the meadow reaches of West Chicken Creek and Limber Jim Creek, respectively. However, these differences were not significant ($P > 0.14$).

During base flow, there were no significant differences in average travel distances among forest, transition, and meadow reaches (P> 0.10, Fisher's LSD multiple comparison tests) in both streams (Table 7). The average base-flow travel distance for all sites ($n = 9$) was 2.9 m (± 1se = 0.9) in West Chicken Creek and 21.8 m (± 3.2) in Limber Jim Creek. When combining data from forest and meadow sites, travel distances of *Ginkgo* leaves were significantly longer ($P < 0.02$) during high flow ($n = 4$) than during base flow ($n = 6$) in both streams.

Hydro-geomorphic and riparian influences on retention

The hydro-geomorphic variables discharge, thalweg velocity, stream width, and thalweg depth explained most of the variation in average travel distances of *Ginkgo* leaves in multiple linear regression models. All other parameters (e.g., large wood volume) were not significant ($P>0.10$) and generally accounted for less than 5% of additional variation when the four hydrological variables were included in analyses. Thalweg depth explained 78% of the variation in all *Ginkgo* travel distances (Fig. 10D), and dominated other hydrological variables when included in models. Simple linear regression showed weak but significant associations with discharge and thalweg velocity but stronger associations with stream width (Fig. 10).

Table 7. Mean travel distances (m) of introduced *Ginkgo* leaves and paper strips for all study reaches. High-flow estimates are averages of two releases and base-flow estimates are averages of three releases per reach. Numbers in parentheses are one standard error.

	West Chicken Creek		Limber Jim Creek	
	Base-flow	High-flow	Base-flow	High-flow
Forest-*Ginkgo*	2.8 (1.2)[a]	21.7 (1.0)[b]	19.8 (1.3)[a]	36.9 (1.4)[b]
Transition-*Ginkgo*	1.6 (0.5)[a]	--	18.3 (6.7)[a]	--
Meadow-*Ginkgo*	5.1 (2.5)[a]	63.4 (14.1)[c]	27.6 (7.6)[a]	74.6 (22.5)[c]
Strips	--	41.9 (0.4)[bc]	--	24.6 (14.6)[bc]

Different superscripted letters indicate significant differences ($P < 0.02$ for West Chicken Creek and $P<0.06$ for Limber Jim Creek). Letters only apply to differences among reaches and between base- and high-flow within streams; no between stream tests were made. (-- no data)

For the base-flow releases, there were distinct patterns among reaches in the percent of leaf retention associated with various structures, though differences were not significant ($P>0.10$)(Fig. 11). Visual identification rates of leaves within the channel ranged from 14 to 79% (mean = 48.9% ± 4.2). In both streams, percent of retention by backwater habitats and streamside herbaceous vegetation (primarily *Carex*) increased downstream. In West Chicken Creek, retention by debris dams, about 50% of leaves retained in forest and transition sites were captured by large and small wood. Percent retention by macrophytes was higher in downstream reaches. In contrast, retention by wood and rocks was dominant in all reaches of Limber Jim Creek (Fig. 11). Leaf retention within pools was minor at all sites.

During high-flow, turbidity and hazardous flow conditions resulted in low identification rates of retained leaves (10-53%; mean = 27.8 ± 4.1). Nevertheless, 33-

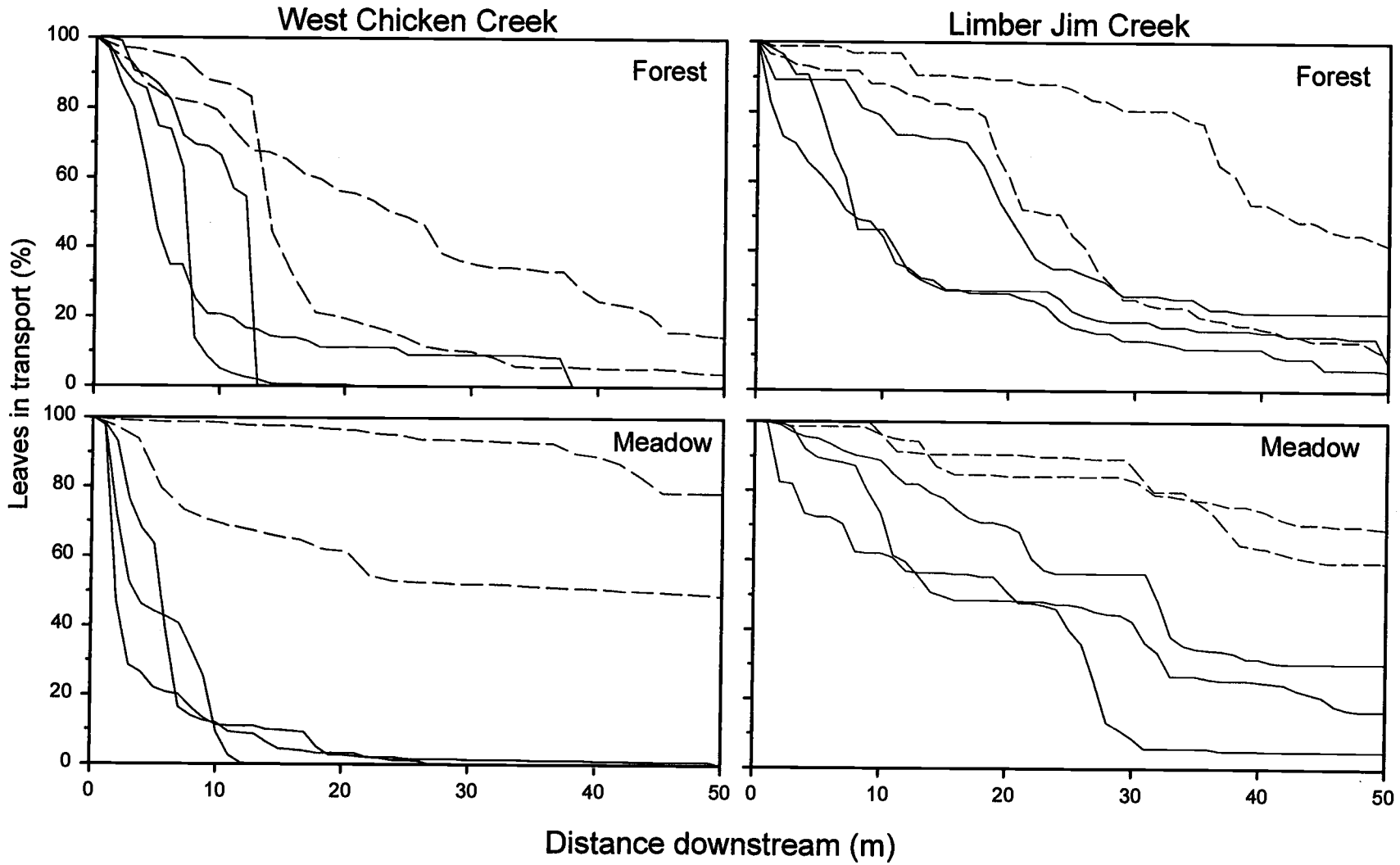

Figure 9. Retention curves for forest and meadow reaches of the study streams during highflow (dashed lines) and during baseflow (solid lines).

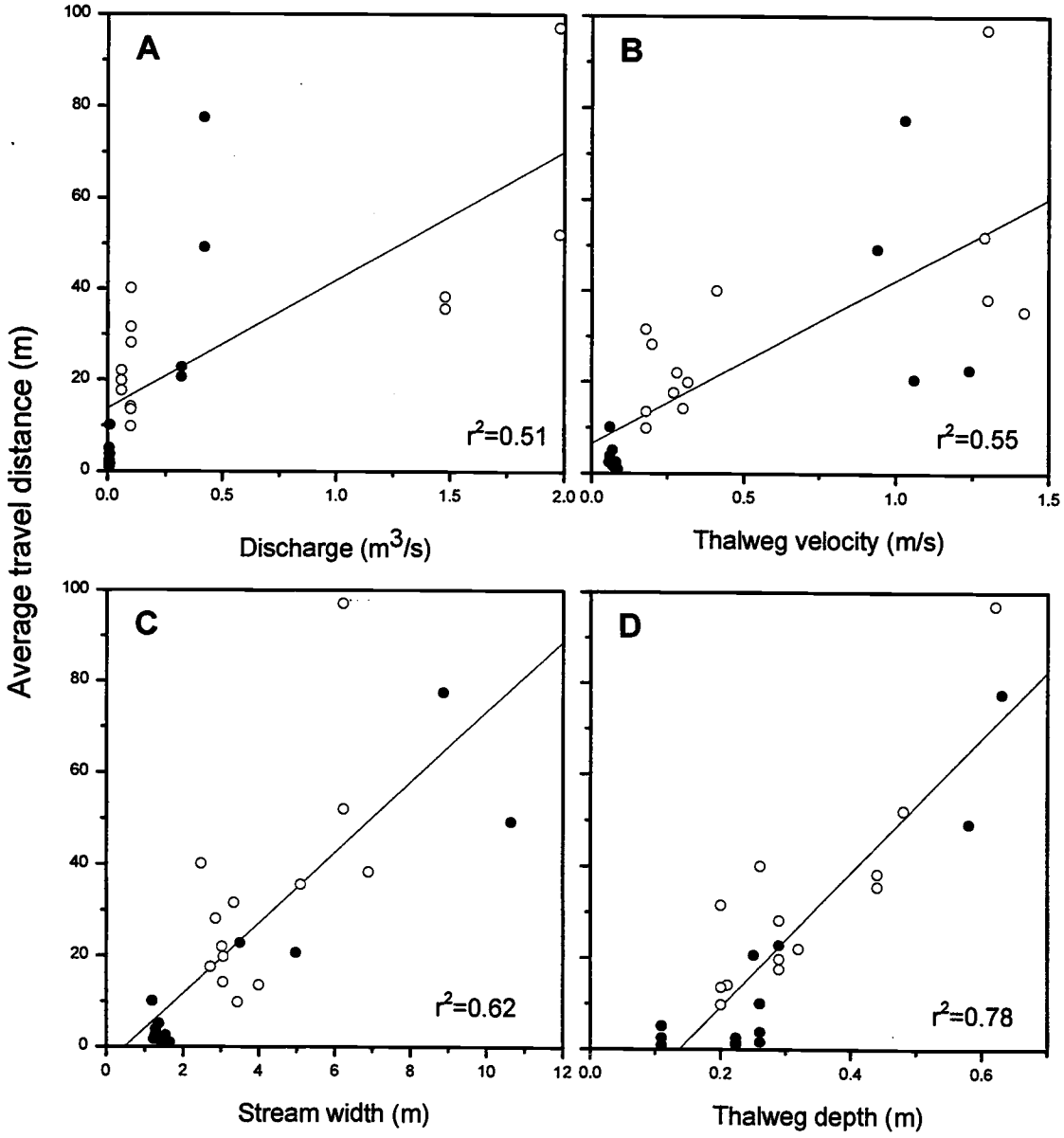

Figure 10. Regressions of average travel distances for all *Ginkgo* releases ($n = 26$) against hydro-geomorphic variables. For all regressions $P<0.001$. Closed circles are releases in West Chicken Creek and open circles are releases in Limber Jim Creek.

54% of observed leaf retention in the forest reaches was associated with large wood and 30-62% was associated with the stems of riparian shrubs (alder and *Ribes* sp.). In the meadow sites of Limber Jim Creek, 27% of retention was associated with large wood, 35% with riparian shrubs (primarily S*alix* spp.), and 35% with streamside sedges. In contrast, 86% of observed leaf retention in the meadow reach of West Chicken Creek was associated with streamside sedges and 13% with in-channel macrophytes (primarily *Fontinalis neomexicana*).

After high-flow waters had receded, we observed that many strips had been transported both laterally and further downstream from their initial location of retention. Paper strips were redeposited onto the active channel and floodplain up to 8 m away from the base-flow channel margin (Fig. 12). The average distance that paper strips traveled onto the floodplain was 1.5 m $\pm$ 0.09 at West Chicken Creek and 0.6m $\pm$ 0.08 at Limber Jim Creek. At West Chicken Creek, 28% of the 1540 strips released were located on the floodplain within the length of our study reach, particularly at meander bends and in high-flow side channels. In contrast, only 5% of released strips were deposited onto the floodplain of Limber Jim Creek, the rest being retained within the channel or exported from the study reach (Fig. 12). However, a few isolated strips were observed >200 m downstream of the release point in both streams, well downstream of the study reach boundaries.

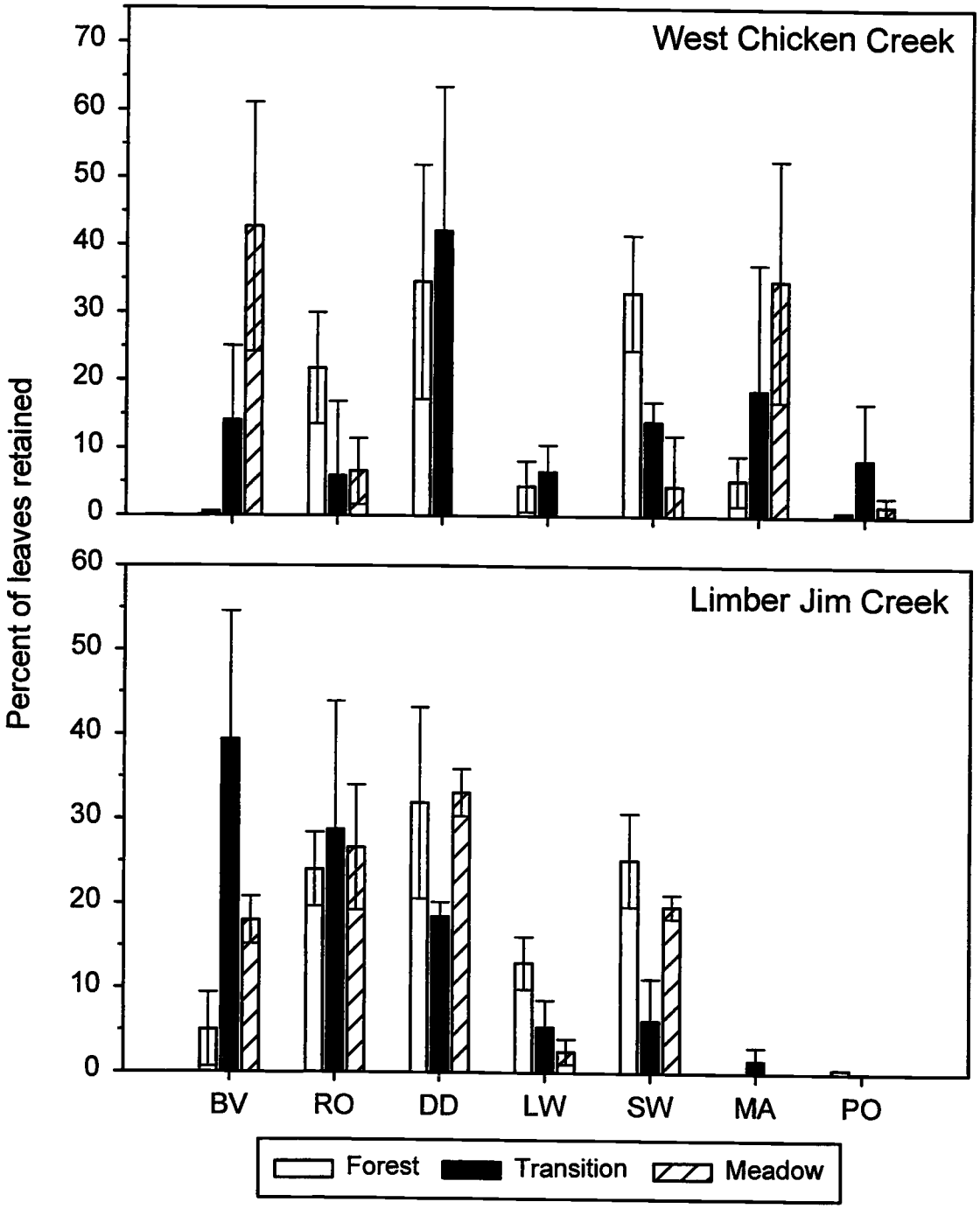

Figure 11. Percent of *Ginkgo* leaf retention associated with various structures during base-flow. Bars are averages ($n = 3$) of release sites within forest, transition, and meadow reaches of the study streams. Vertical lines are one standard error. BV = backwaters and stream-side vegetation, RO = rocks, DD = debris dams, LW = large wood, SW= small wood, MA = macrophytes, and PO = pools.

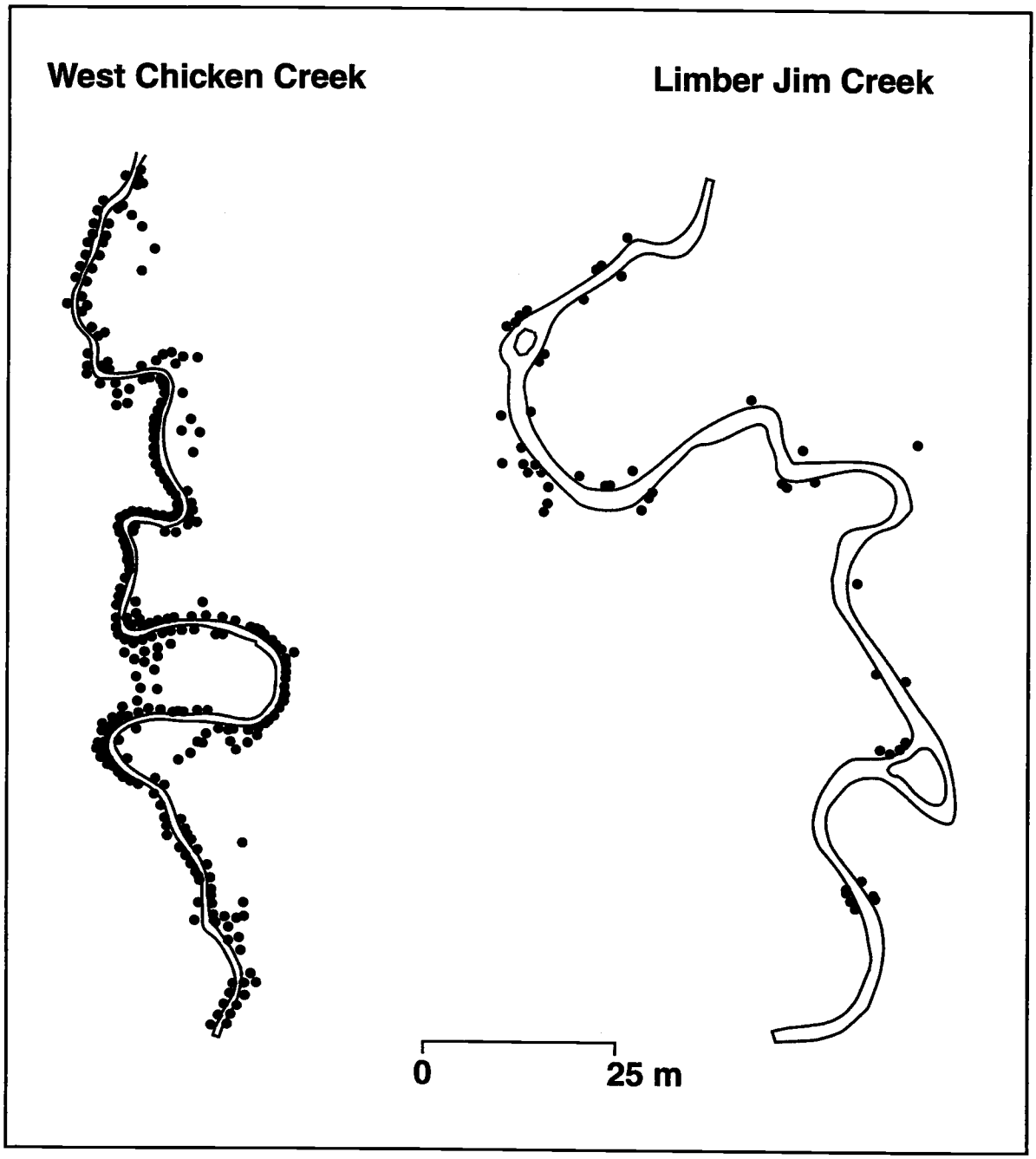

Figure 12. Map of paper strip distribution on the floodplains of the meadow study reaches. Each dot represents the location of one paper strip in July 1998. Strips were released approximately 10m upstream of uppermost dots.

DISCUSSION

Spatial and temporal patterns of retention

Many studies of CPOM retention in low order streams have reported lower retention during periods of elevated discharge and with increases in stream size (Speaker 1985, Webster et al. 1987, Jones and Smock 1991, Snaddon et al. 1992, Scarsbrook and Townsend 1994, Wallace et al. 1995). In our study, Limber Jim Creek had 2.5 - 4.7 times higher discharge than West Chicken Creek. Accordingly, *Ginkgo* retention was consistently lower in Limber Jim Creek than in West Chicken Creek. However, because stream power typically decreases with decreasing channel slope (Gordon 1993), it is probable that stream power per unit area was lower in the meadows than in the forests. Additionally, discharge and thalweg velocity explained little of the variability in average travel distances among reaches (Fig. 10). For example, travel distances were higher in the meadow reach of West Chicken Creek than in the forest reach of Limber Jim Creek despite similar average thalweg velocities (0.94 - 1.03 m/s vs. 0.91 - 1.19 m/s) and much higher discharge in Limber Jim Creek.

We found that average thalweg depth explained the most variation in average travel distances among all *Ginkgo* releases in this study (Fig.10). Similar relationships between CPOM travel distance and stream depth have been reported for small streams in the Cascade (Speaker 1985) and Appalachian Mountains (Webster et al. 1994) and have been attributed to a decreasing frequency of particle collision with obstacles as depth increases. These observations are consistent with numerous studies demonstrating that

CPOM retention in small streams depends on the probability of a particle colliding with an obstruction (e.g., debris dams and rocks) and the probability that the particle will be trapped upon contact with the obstruction (e.g., Young et al. 1978, Speaker et al. 1984, Webster et al. 1987, Ehrman and Lamberti 1992). Although thalweg depth and stream width explained the most variation in travel distances overall, associations with these variables were weak when high-flow releases were excluded from the analysis. This suggests that observed associations between travel distance and stream depth and width are probably reflective of decreases in the frequency of retention structures relative to the size of stream flow during high discharge.

The volume of large wood occupying the active channel decreased downstream from forest to meadow in both streams: from 0.007 $m^3 \cdot m^{-2}$ to 0.0007 $m^3 \cdot m^{-2}$ in West Chicken Creek and from 0.02 $m^3 \cdot m^{-2}$ to 0.009 $m^3 \cdot m^{-2}$ in Limber Jim Creek. Thus, as stream size increases downstream due to tributary inputs, the ratio of discharge, depth, and width to wood volume per unit area also increased. Although we did not estimate the retention efficiency of various retention structures in this study (e.g., Speaker et al. 1984), debris dams and individual pieces of large and small wood accounted for the majority of observed base-flow leaf retention in all reaches except the meadow of West Chicken Creek (Fig. 11). In addition, 22 - 51% of observed leaf retention in the forests during high flow was associated with large wood.

In general, observed associations of leaf retention with accumulations of wood are consistent with patterns of CBOM storage in the two streams; CBOM in fall 1999 was strongly associated with average large wood mass among all study reaches (Chapter 1,

Fig. 7). In fact, 87% of CBOM in the meadow reach of Limber Jim Creek occurred in pools associated with debris dams (Chapter 1). These lines of evidence suggest that large wood abundance strongly influences spatial patterns of CPOM retention and storage in these streams.

A low percentage of released *Ginkgo* leaves were retained within pools (Fig. 11), whereas pools accounted for the majority of CBOM *storage* within most reaches of both streams (Appendix D). Speaker (1985) reported similar disagreement between short-term CPOM retention and longer-term storage within pools in Cascade Mountain streams of Oregon, but also found that a low percentage of released leaves actually reached pools because they were retained by upstream riffle habitats. Because pools are erosional sites created by scour during high flow, low short-term retention but high CBOM storage suggests that retention within pools is a longer term process mediated by CPOM availability, high flow dynamics, and the presence of other retentive features.

We found that CPOM retention during high discharge was strongly influenced by riparian and floodplain vegetation. This is similar to results reported by Speaker et al. (1988), Cuffney (1988), and Jones and Smock (1991). In addition, higher retention rates may occur in unconstrained reaches with complex lateral habitat than in constrained reaches characterized by more linear flow (Lamberti et al 1989). In our study, travel distances were consistently longer in the more extensively flooded meadow reaches. In the forests, 29 - 78% of observed leaf retention occurred on the stems of riparian shrubs (*Ribes* sp. and alder). In the meadows, shrub stem densities were much lower, and thus, most leaves were retained on near-stream sedges and grasses.

Average travel distances were longest in the meadow reaches despite extensive lateral inundation. This suggests that hydraulic roughness created by herbaceous vegetation (primarily *Carex*) in the meadows was sufficiently low to maintain particles in suspension. Roughness coefficients for floodplain vegetation types are generally lowest for deeply inundated flexible grass and highest for dense shrubs like willow (Acrement and Schneider 1989). In our study, roughness was probably low within the active channel where the average depth of stream flow was at least two times the height of sedges (*personal observation*) but higher on the upper floodplain where water depth was much lower. High unexplained variability (38%) in the association between stream width and travel distance suggests that decreases in retention during spring flooding were a reflection of differences among reaches in the trapping efficiency of the dominant riparian vegetation.

Retention within flooded riparian zones is greatly influenced by channel morphology and floodplain surface topography (Cuffney 1988, Jones and Smock 1991). In our study, Limber Jim Creek was the larger, higher velocity stream and flow was confined to a moderately entrenched active channel. In contrast, West Chicken Creek spreads out laterally as shallow over-bank flow. To illustrate this, discharge in the meadow reaches during high-flow was 2.5 - 4.7 times higher in Limber Jim Creek, yet average stream width was nearly twice as wide in West Chicken Creek. Therefore, in the meadows, differences in power and geomorphic constraint likely control movement rates of CPOM between stream and floodplain.

CPOM storage in streams is not determined simply by short-term retention probabilities but also by the probability that a particle is retained in a given location for

longer periods of time. With increases in flow, leaves can be dislodged from obstacles and transported further downstream (Young et al. 1978, Speaker et al. 1984). In addition, increases in discharge can move CPOM from stream channels to adjacent floodplains where it is then retained (Jones and Smock 1991). In our study, ~12% of paper strips introduced into the meadow reaches of West Chicken Creek were exported downstream within three hours of release, the majority being retained within 42 m of the release point. However, approximately one month after floodwaters had receded, we found that 28% of the paper strips introduced into the channel had been deposited onto the active channel and floodplain (Fig. 12).

Because high-flow releases were conducted during a dip in the rising limb of the hydrograph (Appendix A), it is likely that some strips initially retained within the channel were dislodged and laterally displaced during peak flow. Apparently, paper strips were trapped on the floodplain by grasses and sedges as water became increasingly shallow during the falling limb of the hydrograph. In contrast, deposition of paper strips on the floodplain in the meadow reach of Limber Jim Creek was relatively minor (Fig. 12). In combination with longer *Ginkgo* travel distances, low deposition in lateral areas is a further indication that high stream power and a more entrenched channel may result in the downstream export of much of the CPOM entering Limber Jim Creek during spring flooding (Chapter 1).

Retention and the fate of riparian detritus

Over the course of this study, the vast majority of detritus entering the meadow reaches of West Chicken Creek and Limber Jim Creek was herbaceous material entrained by the streams during spring flooding (Chapter 1). In contrast, annual riparian inputs to the forest reaches were dominated by litterfall and lateral movement composed primarily of needles, woody material, and alder leaves. In the forests, peak detrital inputs occurred in the fall due to alder leaf fall and larch needle drop (Chapter 1, Figure 3). Thus, in the forests, peak detrital input rates occurred during the period of highest CPOM retention, whereas peak inputs in the meadows occurred during the period of lowest retention and maximum CPOM export (Chapter 1). However, the results of our paper strip releases suggest that lower retention within the channel may ultimately increase the probability of floodplain deposition downstream.

Spatial patterns of retention were consistent with longitudinal decreases in CBOM in the two streams (Chapter 1, Figure 6). High levels of retention in the forest and transition reaches during alder leaf fall probably result in very little export of leaf CPOM to downstream reaches Moreover, because alder leaves have fast decomposition rates and may be an important food source to shredding macroinvertebrates (Sedell et al. 1975), it is likely that downstream transport of this labile source of organic matter is a minor coarse particulate supplement to meadow reaches. In contrast, alder leaves falling from August to October comprised the majority of broad leaf CPOM inputs and particulate nitrogen entering the forest reaches on an annual basis (Chapter 1). However, conifer needles and woody material dominated annual CPOM inputs to the forests, tissues that

decompose relatively slowly (Sedell et al. 1975, Mellilo et al. 1983). In addition, most of the CPOM stored within all the study reaches of both streams consisted of woody material and needles (Chapter 1). Therefore, higher CBOM storage in the forests are probably a result of both higher retention and slower decomposition rates of dominant CPOM tissues.

In the meadows, graminoid tissues were exported downstream or deposited onto the floodplain during spring flooding. Graminoid tissues are generally considered a poor food source for aquatic invertebrates (Scarsbrook and Townsend 1994). However, because of low levels of structural carbon (e.g., lignin) herbaceous material would likely decompose faster than conifer needles and woody material (Webster and Benfield 1986). Indeed, we found that the mean C:N ratio of sedge tissues in the meadows (42) was much lower than the mean C:N ratio of needles and woody material (63) in the forests (Chapter 1). In addition, lignin concentrations of needles and woody material range from ~24 – 50% (Triska et al. 1975, Melillo et al. 1983) compared to lignin concentrations of sedges which are generally < 7% (Aerts et al. 1997). These lines of evidence further suggest faster decomposition rates in the meadow reaches than in the forest reaches. Furthermore, calculated turnover times of CPOM in the forest reaches were 0.43 y and 0.96 y compared to 0.05 y and 0.26 y in the meadow reaches, at West Chicken Creek and Limber Jim Creek, respectively (Chapter 1). Thus, it is likely that redistribution and fragmentation of sedge litter occurring during high-flows influences floodplain soil organic matter formation.

High physical retention, coupled with low to moderate biological processing rates, is expected to contribute to energetic stability in headwater reaches. Within a stream

network, the relative availability of retention structures generally decreases downstream, resulting in more conduit-like mid-order reaches where export predominates over storage (Minshall et al 1983, 1992). Although the annual loading of organic matter was estimated to be higher in the meadow reaches than in the forest reaches of both streams (Chapter 1, Table 2), CPOM inputs were likely rapidly decomposed, deposited onto the floodplain, or exported downstream. It is likely that longitudinal shifts from forests to small herbaceous floodplains influence larger scale patterns of organic matter flow in the Upper Grande Ronde River Basin. In combination with our study of organic matter dynamics in the two streams (Chapter 1), this study illustrates the importance of understanding the influences of reach and valley-segment scale variation in hydro-geomorphic and riparian characteristics on spatial and temporal patterns of detrital movement in headwater stream ecosystems.

CHAPTER 4

CONCLUSIONS

The results of this study suggest that inclusion of high-flow detritus inputs, consideration of reach-scale geomorphology and detrital quality, and examination of temporal and spatial dynamics of physical retention is important to the development of a broader conceptual framework of organic matter flow in headwater streams and riparian zones. Few studies have combined analyses of inputs, input quality, transport, retention, and storage to describe organic matter dynamics in headwater stream ecosystems. Also, studies of longitudinal patterns in CPOM input and movement over relatively small scales are uncommon; most studies of longitudinal patterns have investigated changes over increases in stream order (e.g., Vannote et al. 1980, Minshall et al. 1983, Naiman et al. 1987, Minshall et al. 1992). Moreover, most of these studies used single, small (< 100m) reaches to represent the ecosystems of entire stream orders. Our finding of large differences among study reaches within headwater streams suggests that inclusion of reach scale heterogeneity in riparian and geomorphic characteristics is a critical element in the design of lotic ecosystem studies.

The quantity, quality, and timing of detritus inputs, and the processes by which it entered the streams, differed between forest and meadow reaches. In addition, the rate at which CPOM was retained varied seasonally and among reaches depending on reach - level hydro-geomorphic characteristics and riparian vegetation. These differences resulted in pronounced longitudinal patterns of CPOM transport and storage. Although replication was low in our study, our results suggest that coniferous forests and floodplain

meadows may be end member ecosystems along a gradient of detrital quality, import processes, movement rates, and storage. In general, coniferous forest reaches can be characterized as low detrital quality, high CPOM diversity, litterfall/lateral and wind-throw import processes, high retention/low movement rate, and high storage systems. Meadow reaches can be characterized as moderate quality, spring flood import, low retention/ high movement rate, and low storage systems.

There are at least two major exceptions to this generalization: 1) there were no longitudinal differences in retention during base-flow; and 2) the highest quality (high N, low C:N ratio) CPOM inputs (alder leaves) were found in the forest reaches. However, it is important to note that the majority of CPOM movement in our study occurred during high-flow (Chapter 2) as is the case in most small streams (Fisher and Likens 1973). Also, alder leaves were a significant input to the forests for only three months out of the year; the vast majority of CBOM in the forest reaches was woody material and needles. This underscores the importance of seasonal variation in stream flow and plant phenology to the organic matter dynamics of headwater stream ecosystems. It is likely that the abundance and distribution of aquatic consumers are influenced by these reach level differences in CPOM availability (e.g., shredding macroinvertebrates responding to fall alder leaf inputs). Disturbance processes and variation in geomorphology can produce riparian patchiness that, in turn, may control the structure and function of aquatic communities over various temporal scales (Minshall et al 1988, Pringle et al. 1988). For example, Molles (1982) found major differences in Trichopteran assemblages related to differences in riparian organic matter inputs between stream reaches dominated by coniferous forests and reaches dominated by post-fire aspen communities.

Of particular significance in our study was the quantification of high-flow CPOM inputs. In their synthesis of organic matter budgets of 35 streams, Webster and Meyer (1997) indicated that one of the most frequently missing budget components was floodplain particulate inputs. In our study, we have demonstrated that up to 98% of annual inputs of detritus to meadow stream reaches were derived from adjacent herbaceous-dominated floodplains. Even in the forest reaches, where the majority of inputs were from litterfall and lateral movement, over 20% of annual input was of herbaceous material imported during spring high-flow. Similarly, Bilby and Bisson (1992) found that ~ 14% of annual allochthonous inputs to both clear-cut and old-growth coniferous forest streams in Washington were composed of herbaceous material that was captured during winter high-flows. Because herbaceous material is imported relatively rapidly and generally differs in chemical quality from litterfall, exclusion of high-flow inputs from organic matter budgets may lead to erroneous conclusions about energy and material flow in stream ecosystems.

The results of our study are consistent with the general idea that landform features and associated geomorphic processes are major determinants of stream and riparian ecosystem expression (Montgomery 1999). Riparian soils in the floodplain meadow reaches are composed of alluvial silts and clays. It is likely that much of the soil composing the stream banks and influencing channel morphology in the meadow reaches is ancient volcanic ash delivered via fluvial transport from upstream and adjacent uplands (Harward and Youngberg 1970). This hypothetical developmental history is consistent with the dominance of graminoid plants, particularly *Carex*, on fine-textured sediments in meadow systems of the Upper Grande Ronde Basin (Crowe and Clausnitzer 1997).

Therefore, it seems that volcanism and sediment transport may have produced the floodplain landforms present today, and thus, the importance of seasonal flooding to allochthonous organic matter dynamics in these systems.

Our study has several implications for the management of headwater riparian and stream ecosystems. In particular, livestock grazing could strongly influence the patterns and processes we have investigated. Livestock can remove a large amount of herbaceous biomass from floodplains that otherwise would be incorporated into riparian and stream ecosystems. Also, livestock grazing can influence channel morphology and bank stability, resulting in channel widening or incision (Kauffman et al. 1997). Bank erosion, channel widening, and incision could all result in plant community and productivity changes and facilitate hydrologic isolation of floodplains. Similarly, logging practices can result in major changes in organic matter flow in stream ecosystems (Gregory et al. 1991). Perhaps the most general management implication of our study is one of perspective. Managers must recognize that stream and riparian ecosystems are characterized by spatial and temporal heterogeneity that is biologically meaningful. In particular, it seems that there is a general reluctance to accept the fact that not all headwater streams are forested. Coniferous forests, floodplain meadows, willow floodplains, and many other native riparian types are all ecologically important, have intrinsic value, and require protection, intelligent management, and further study. Indeed, this ecological variation was part of the historical habitat template for now-endangered salmon and steelhead populations. Better understanding and management of these ecosystems is essential to maintaining and restoring biodiversity.

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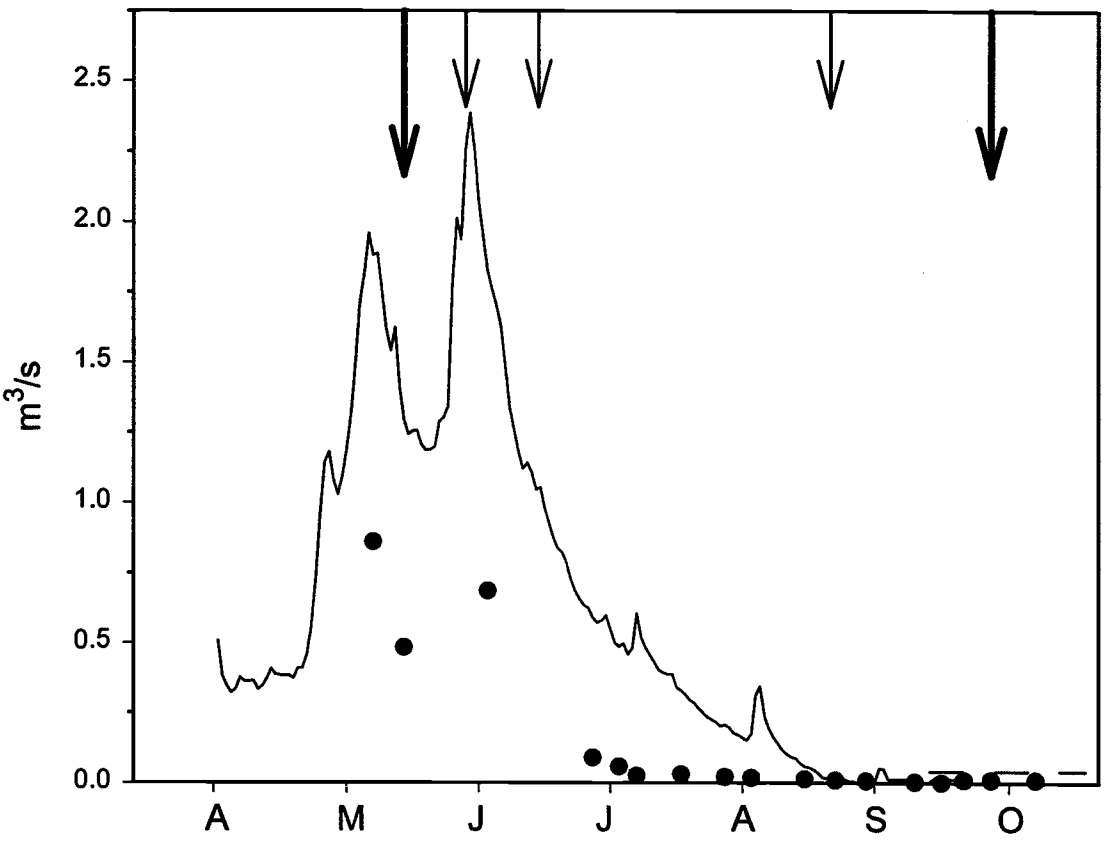
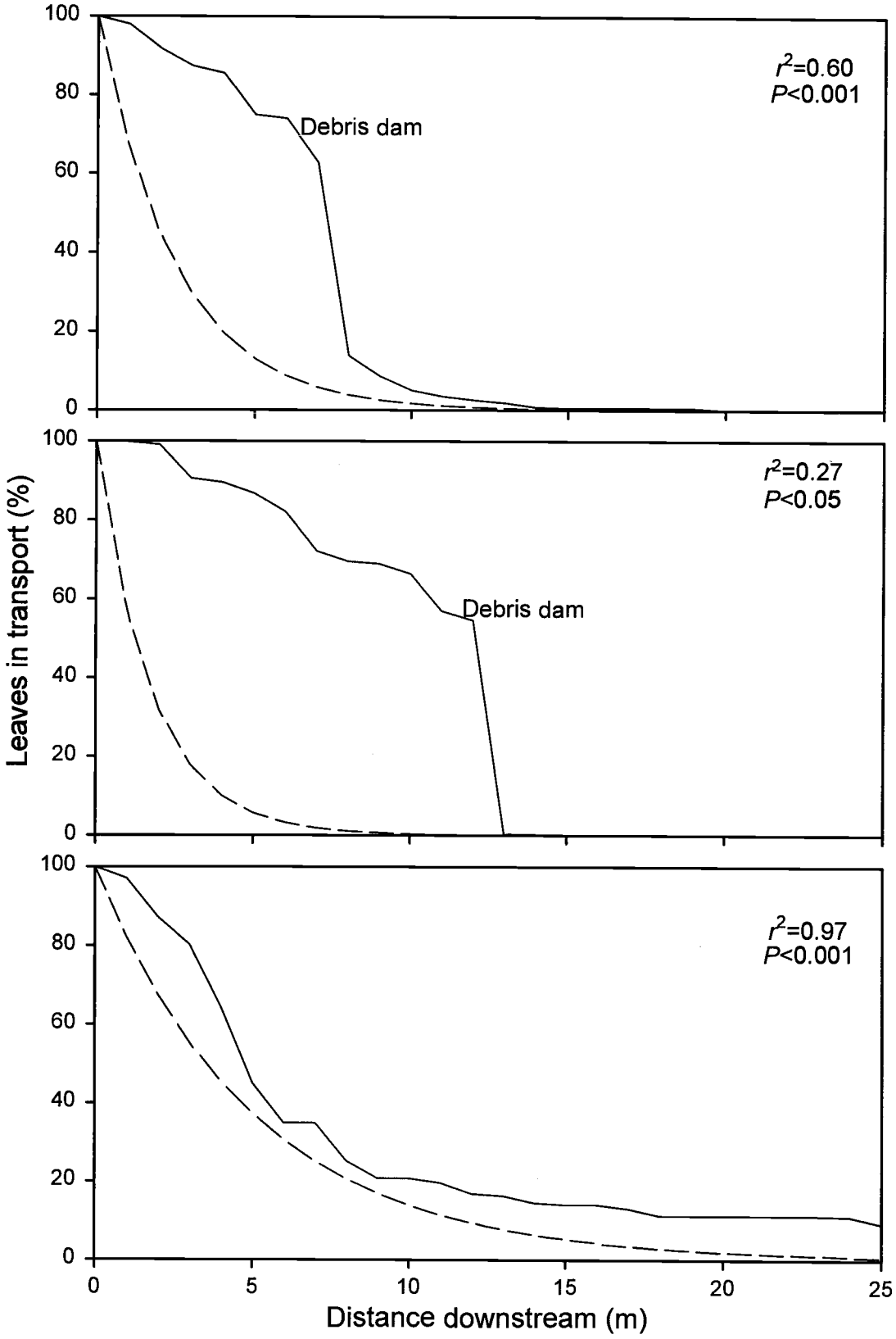
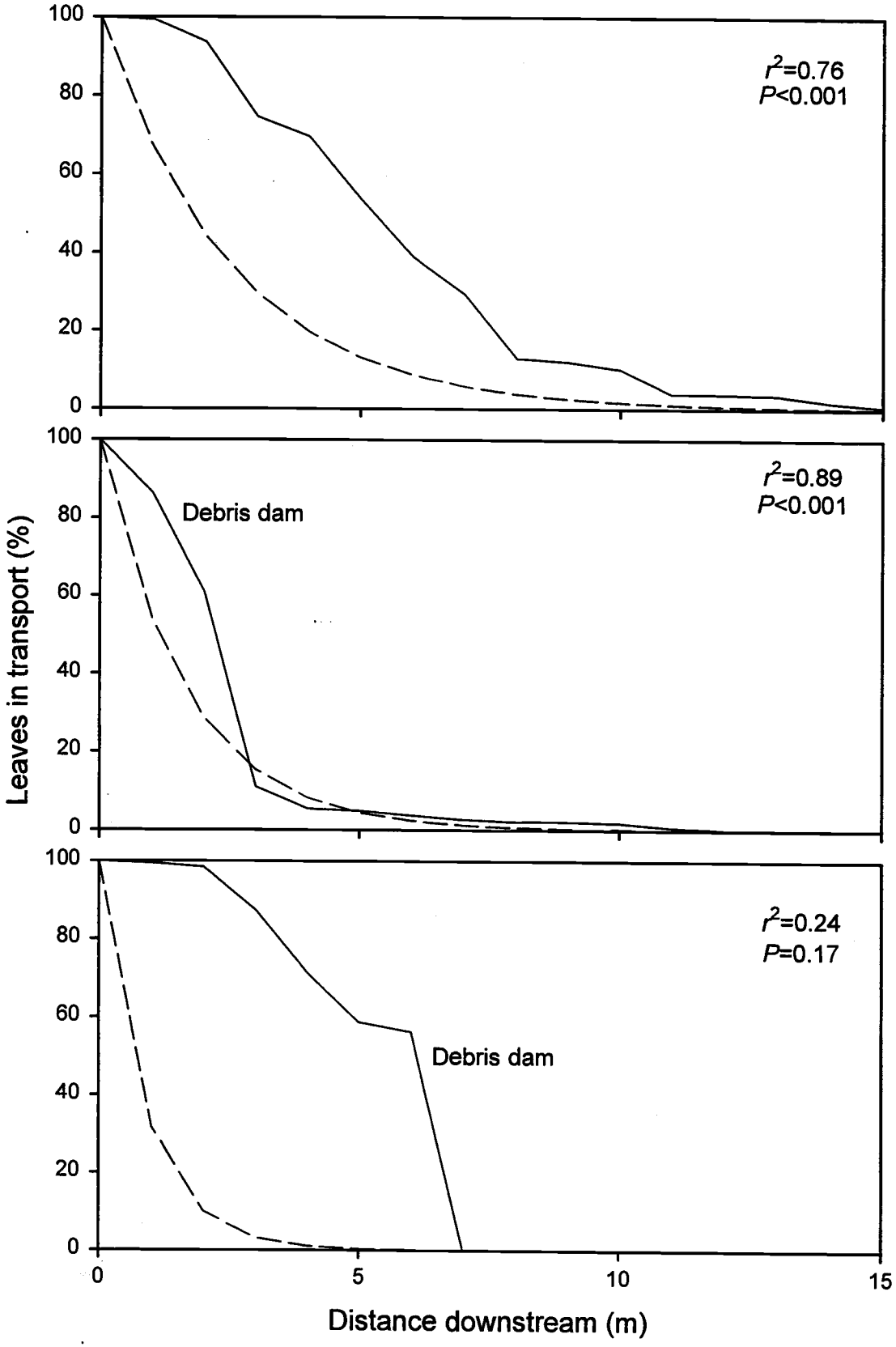
APPENDIX



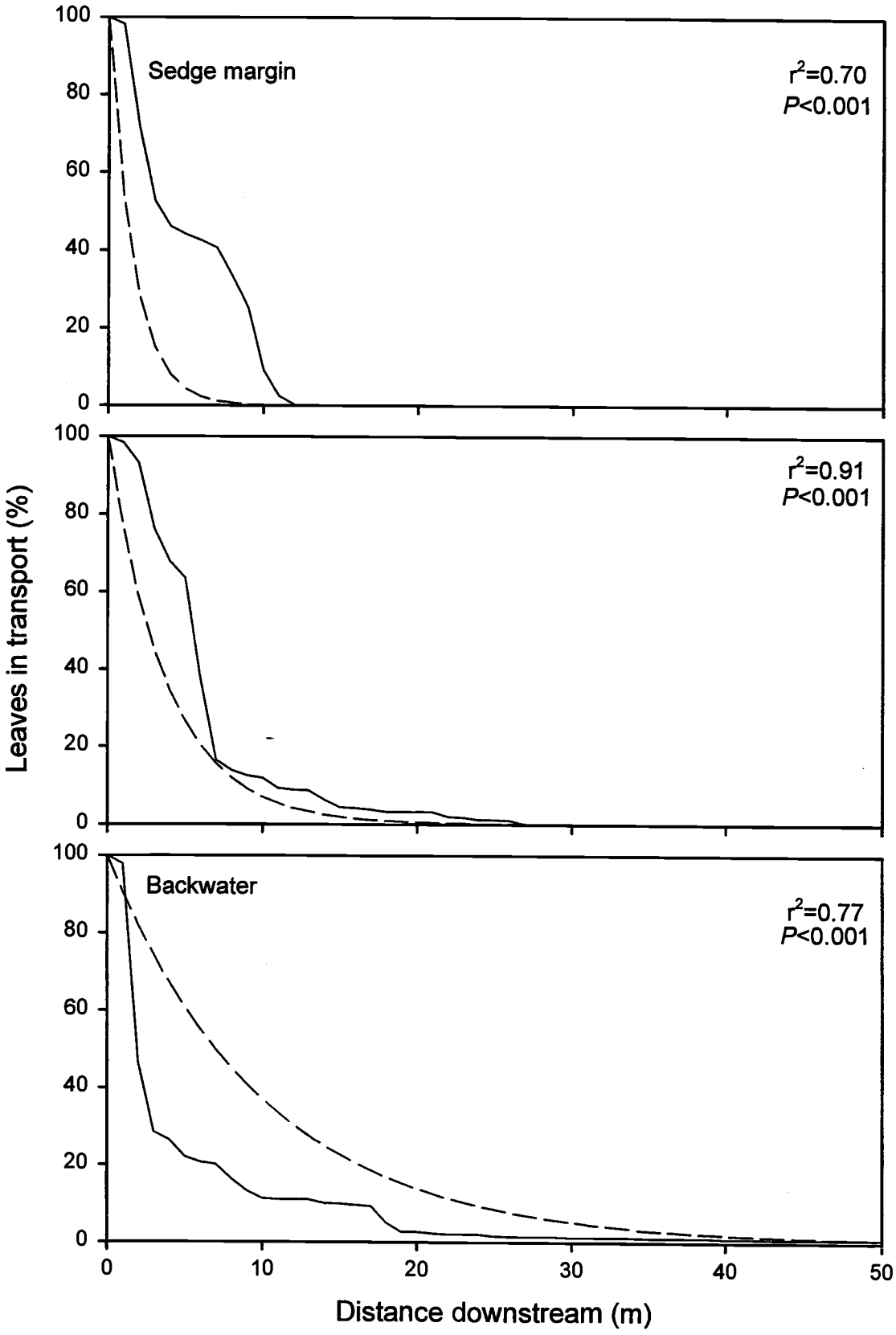
Appendix A. Discharge in the downstream meadow reaches of West Chicken Creek (circles) and Limber Jim Creek (line) for August - October 1998. Data was continuous for Limber Jim Creek but discrete forWest Chicken Creek. Small arrows indicate sampling dates for CPOM transport and large arrows indicate approximate dates of leaf releases. Discharge data was collected by the USFS La Grande.



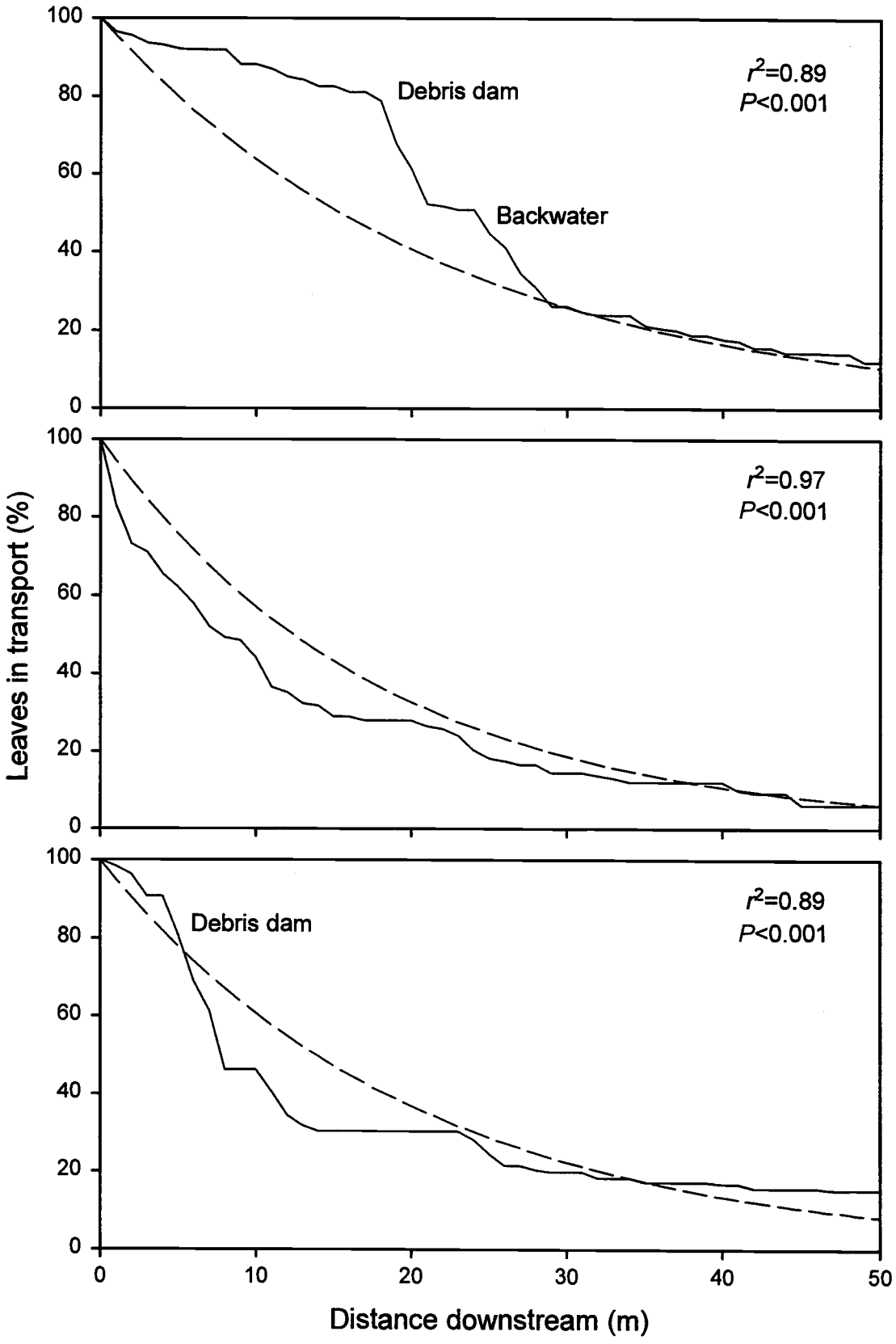
Appendix B1. Baseflow retention curves for the three release sites in the forest reach of West Chicken Creek. Solid lines are survey curves and dashed lines are model curves for Appendix B.



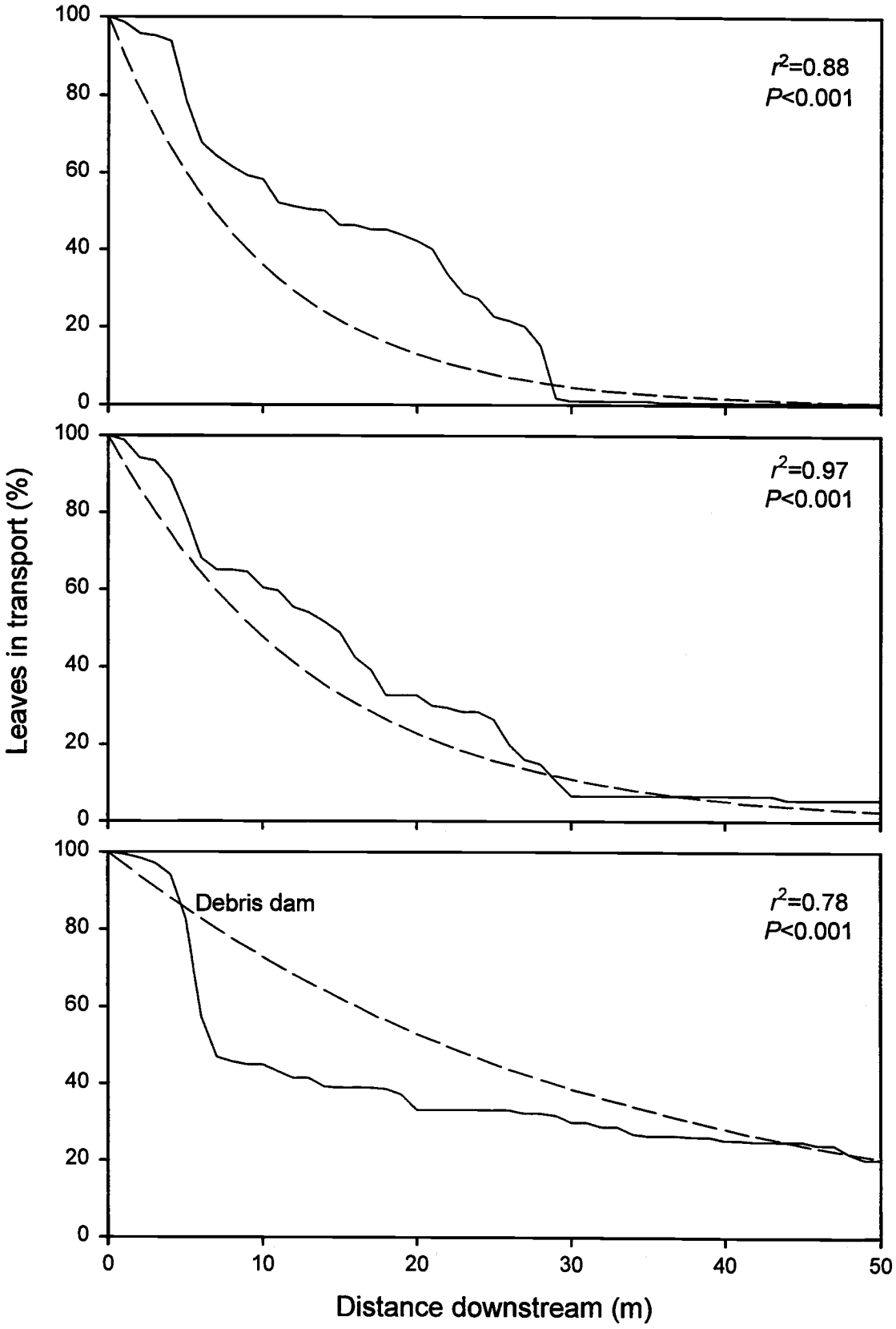
Appendix B2. Baseflow retention curves for the three release sites in the transition reach of West Chicken Creek.



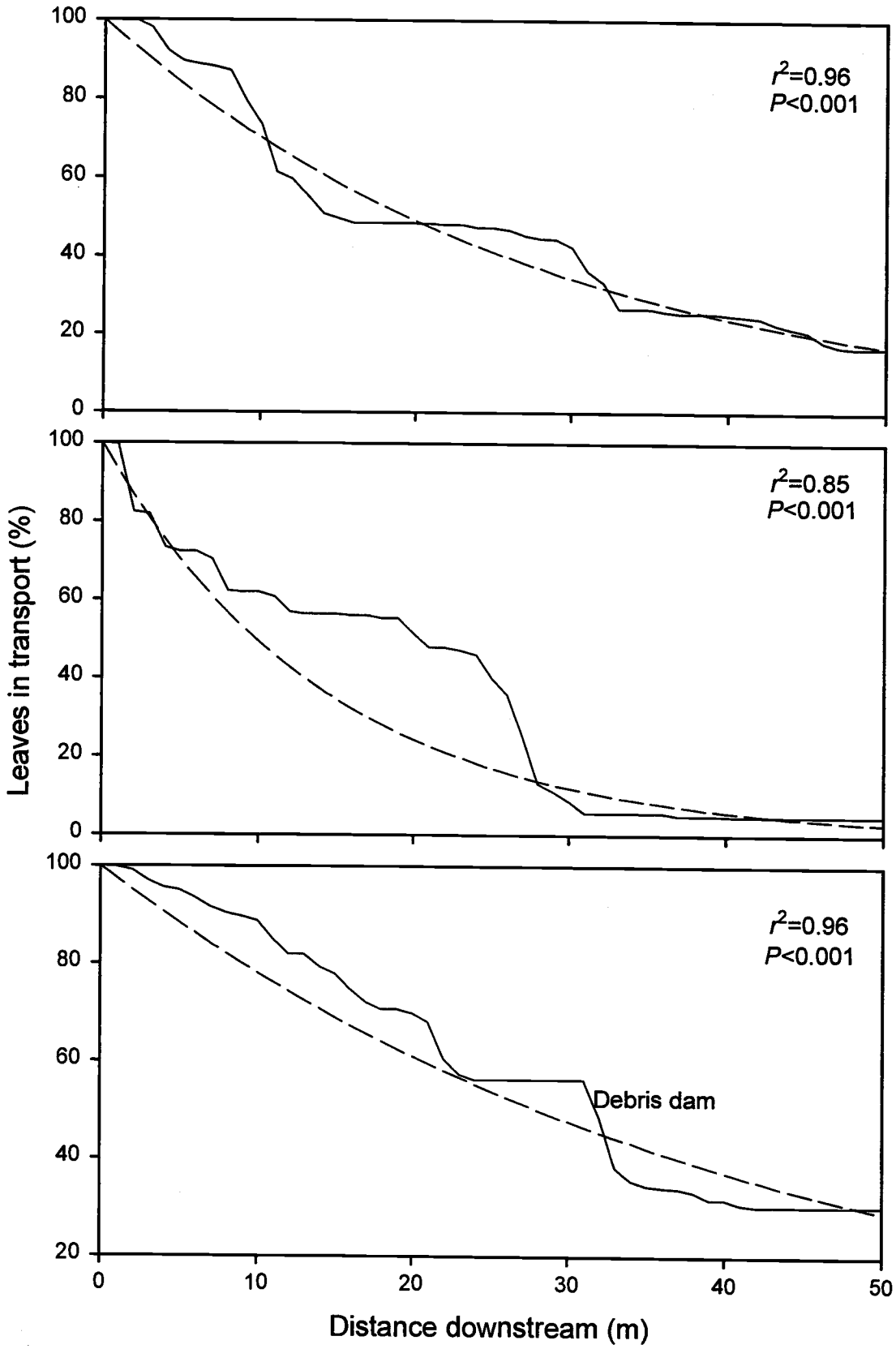
Appendix B3. Baseflow retention curves for the three release sites in the meadow reach of West Chicken Creek.



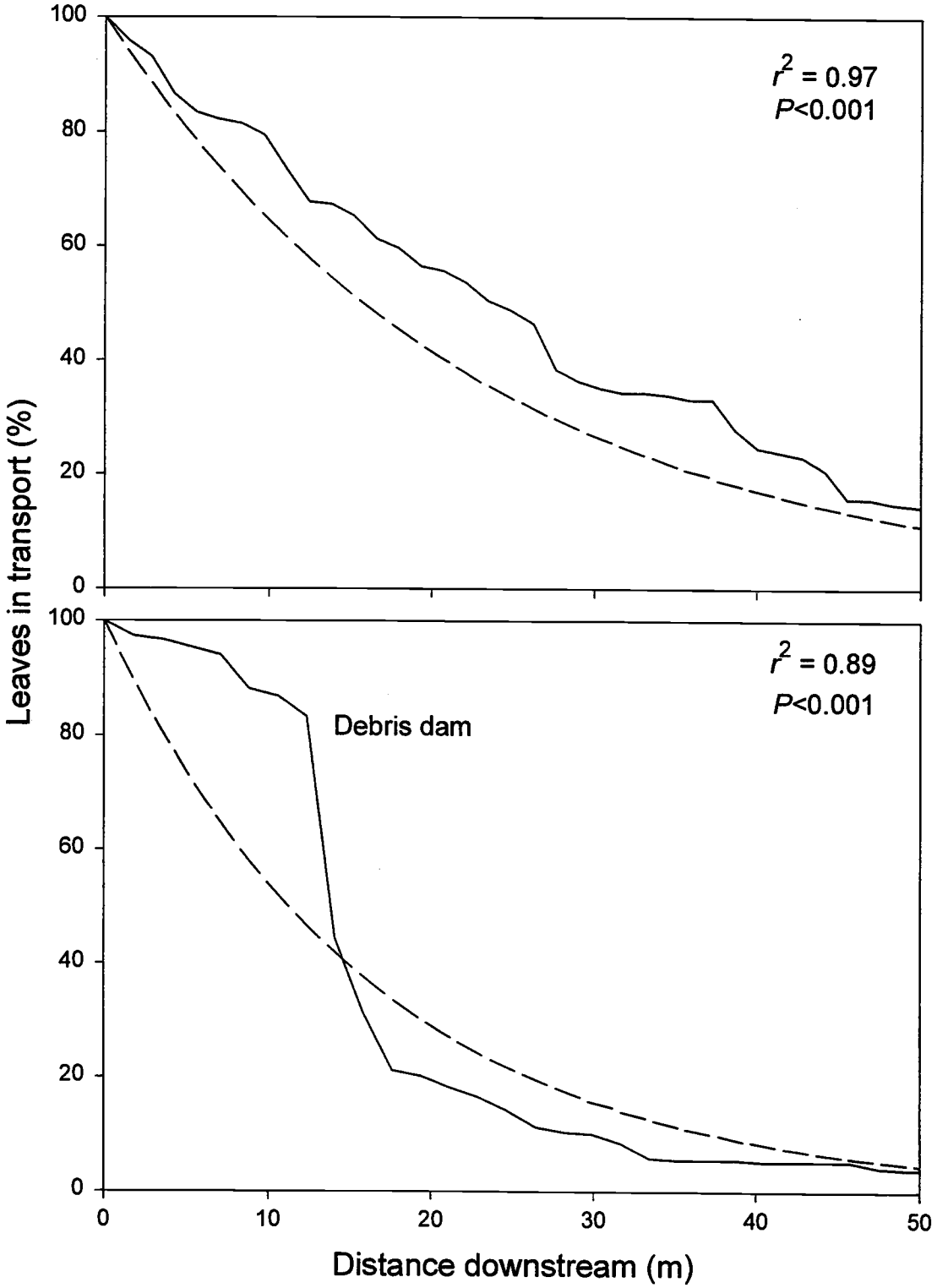
Appendix B4. Baseflow retention curves for the three release sites in the forest reach of Limber Jim Creek.



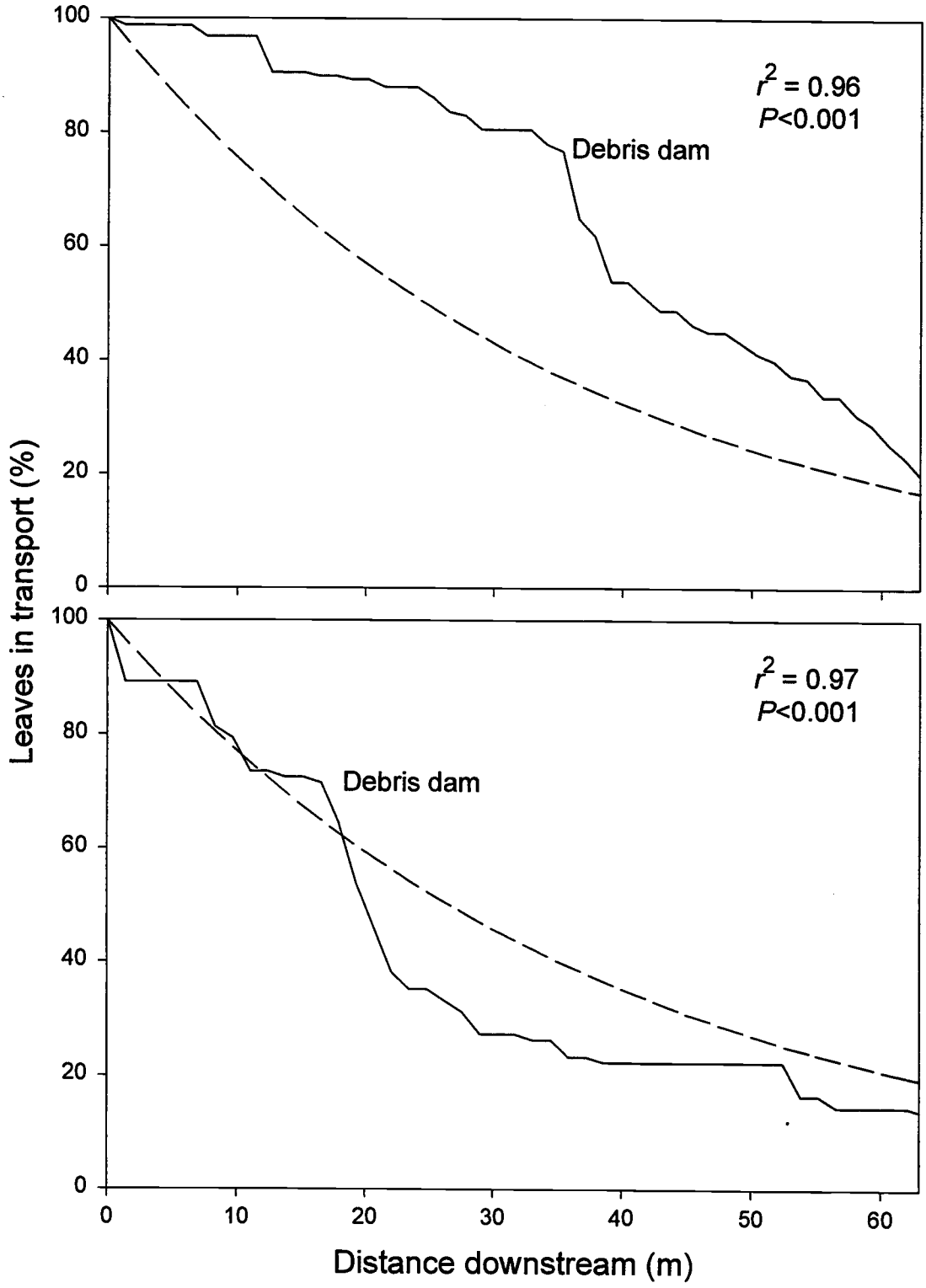
Appendix B5. Baseflow retention curves for the three release sites in the transition reach of Limber Jim Creek.



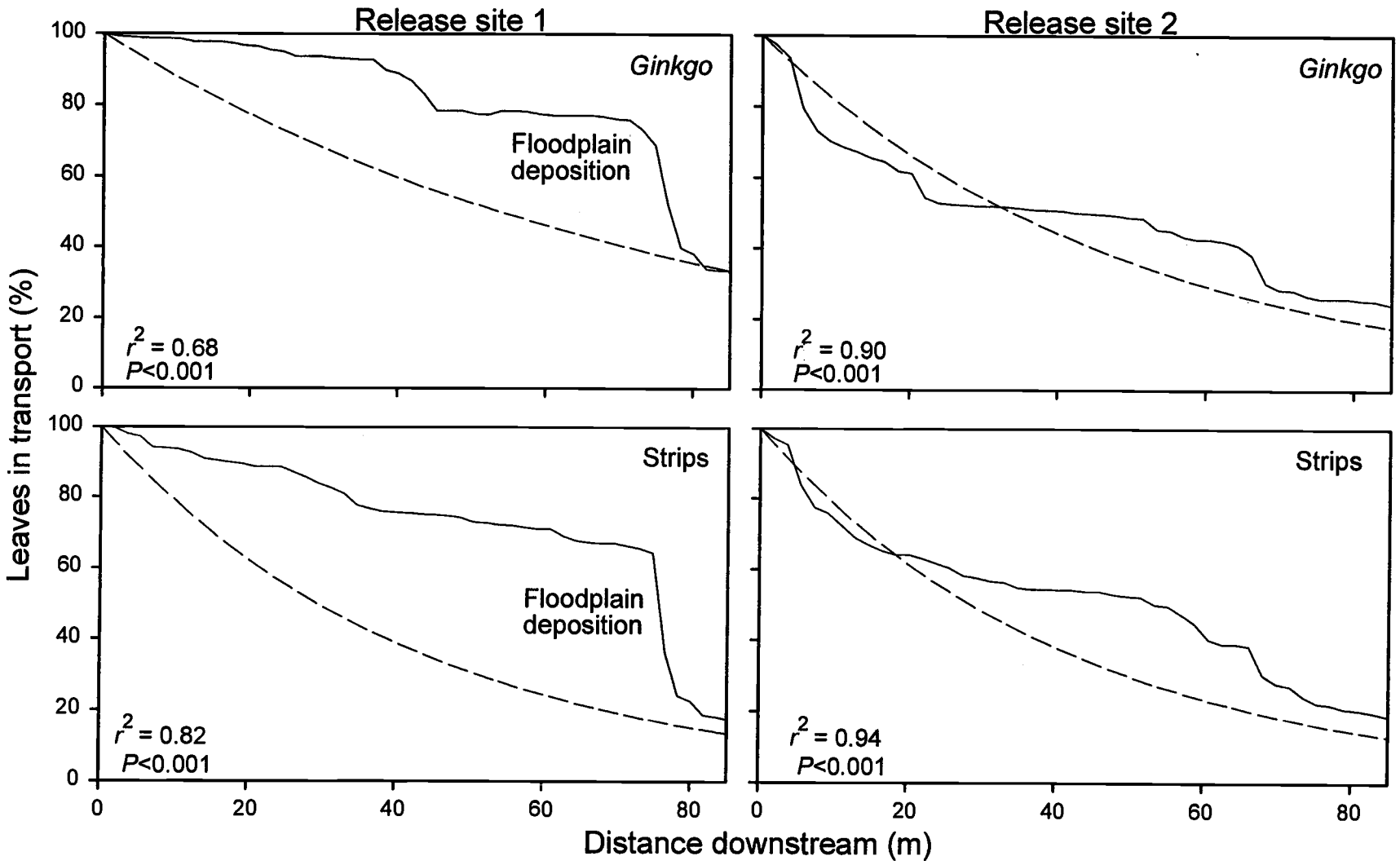
Appendix B6. Baseflow retention curves for the three release sites in the meadow reach of Limber Jim creek.



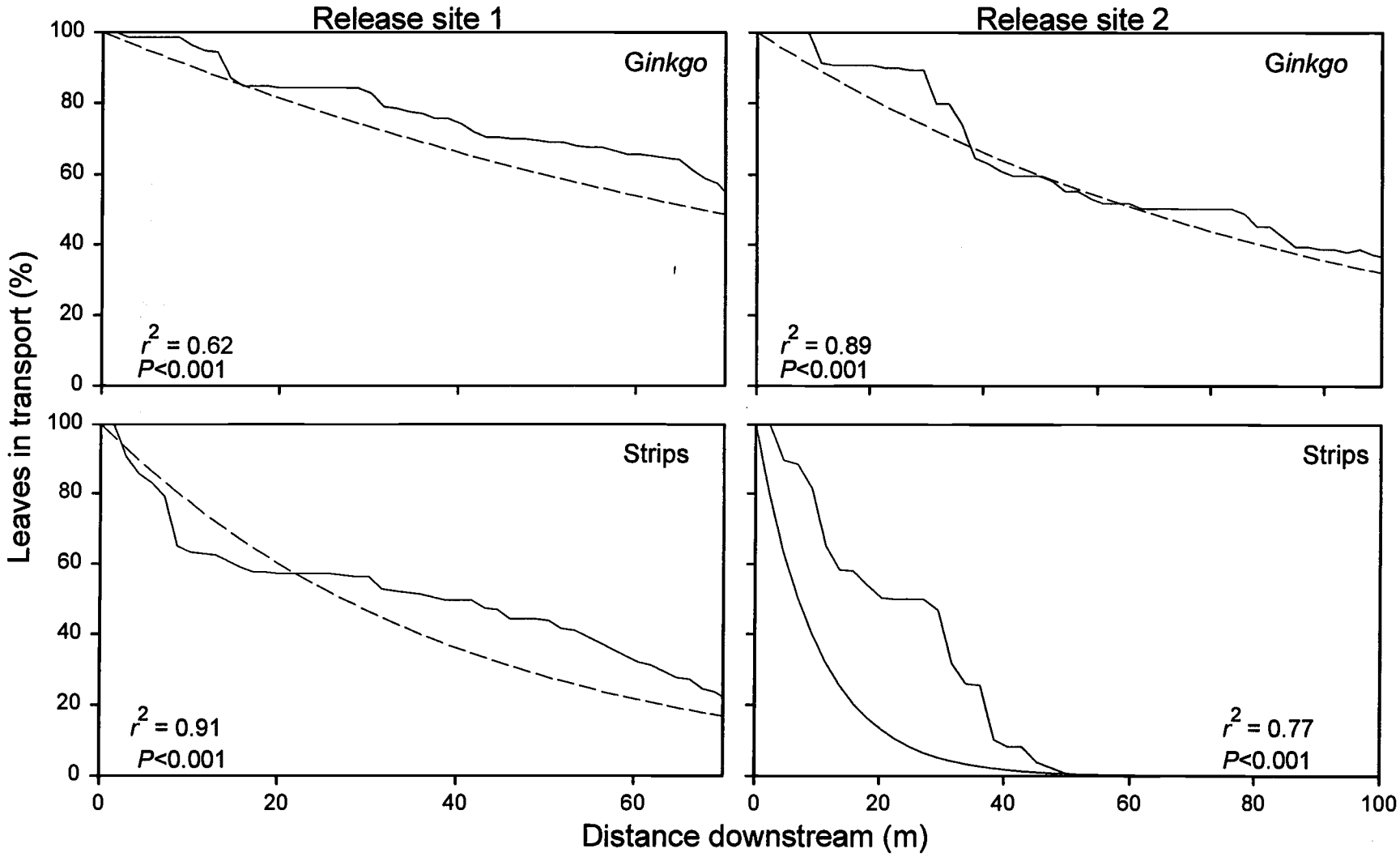
Appendix B7. Highflow retention curves for the two release sites in the forest reach of West Chicken Creek. Survey curves are solid lines and model curves are dashed.



Appendix B8. Highflow retention curves for the two release sites in the forest reach of Limber Jim Creek.



Appendix B9. Highflow retention curves for *Ginkgo* leaves and paper strips in the meadow reach of West Chicken Creek.



Appendix B10. High flow retention curves for *Ginkgo* leaves and paper strips in the meadow reach of Limber Jim Creek.

Appendix C1. Summary of annual AFDM, carbon, and nitrogen inputs (g m^{-2} yr^{-1}) to the forest reach of West Chicken Creek. Included are input estimates per meter of stream length. Numbers in parentheses are one standard error.

	Tissue	AFDM	Carbon	Nitrogen
West Chicken Creek				
litterfall	Alder leaves	22.3 (17.1)	11.7 (8.9)	0.5 (0.4)
	Alder bud scales	1.1 (0.7)	0.6 (0.3)	0.03 (0.02)
	CTBW	40.4 (6.7)	21.4 (3.5)	0.3 (0.1)
	Lichen	9.6 (1.0)	4.4 (0.5)	0.1 (0.02)
	Miscellaneous	6.7 (1.2)	3.5 (0.6)	0.1 (0.02)
	Needles	42.9 (9.7)	22.5 (5.2)	0.3 (0.1)
lateral	Alder leaves	0.4 (0.2)	0.2 (0.1)	0.01 (0.01)
	CTBW	17.1 (2.5)	9.1 (1.5)	0.1 (0.02)
	Herbaceous	0.3 (0.2)	0.1 (0.08)	0.005 (0.003)
	Lichen	2.3 (0.5)	1.1 (0.1)	0.03 (0.004)
	Miscellaneous	2.2 (0.4)	1.1 (0.2)	0.04 (0.01)
	Needles	15.6 (16.3)	8.2 (1.9)	0.1 (0.03)
loading per meter	Alder leaves	34.8 (27.9)	18.2 (13.9)	0.8 (0.6)
	Alder bud scales	2.2 (1.0)	1.1 (0.6)	0.05 (0.03)
	CTBW	88.6 (11.3)	47.0 (7.7)	0.7 (0.1)
	Herbaceous	0.4 (0.2)	0.2 (0.1)	0.01 (0.003)
	Lichen	18.4 (1.4)	8.5 (0.9)	0.3 (0.03)
	Miscellaneous	13.8 (2.0)	7.3 (1.2)	0.3 (0.05)
	Needles	90.3 (16.4)	47.3 (10.9)	0.7 (0.1)

Appendix C2. Summary of annual AFDM, carbon, and nitrogen inputs (g m^{-2} yr^{-1}) to the forest reach of Limber Jim Creek. Included are input estimates per meter of stream length. Numbers in parentheses are one standard error.

	Tissue	AFDM	Carbon	Nitrogen
Limber Jim Creek				
litterfall	Alder leaves	59.2 (17.3)	30.9 (8.9)	1.7 (0.5)
	Alder bud scales	2.1 (0.6)	1.1 (0.3)	0.1 (0.01)
	CTBW	19.0 (1.8)	10.1 (0.9)	0.1 (0.01)
	Lichen	7.4 (1.2)	3.4 (0.5)	0.1 (0.02)
	Miscellaneous	6.9 (1.2)	3.6 (0.6)	0.1 (0.02)
	Needles	26.0 (10.6)	13.6 (5.6)	0.2 (0.1)
lateral	Alder leaves	4.6 (2.1)	2.4 (0.7)	0.1 (0.03)
	Alder bud scales	0.1 (0.01)	0.05 (0.01)	0.002 (0.001)
	CTBW	12.3 (2.1)	6.5 (0.6)	0.1 (0.01)
	Herbaceous	0.2 (0.1)	0.1 (0.04)	0.003 (0.001)
	Lichen	0.8 (0.2)	0.4 (0.1)	0.01 (0.002)
	Miscellaneous	1.4 (0.2)	0.8 (0.1)	0.03 (0.005)
	Needles	8.2 (2.3)	4.3 (1.7)	0.1 (0.03)
loading per meter	Alder leaves	187.8 (50.8)	98.2 (28.5)	4.6 (1.3)
	Alder bud scales	6.8 (1.8)	3.6 (0.9)	0.2 (0.04)
	CTBW	92.3 (8.3)	48.9 (4.4)	0.8 (0.1)
	Herbaceous	0.5 (0.1)	0.3 (0.1)	0.01 (0.004)
	Lichen	24.5 (3.9)	11.3 (1.8)	0.4 (0.05)
	Miscellaneous	24.6 (3.4)	12.9 (2.2)	0.5 (0.1)
	Needles	100.7 (32.5)	52.8 (21.6)	0.8 (0.3)

Appendix D1. CBOM storage (g/ m^2) in forest, transition, and meadow reaches of West Chicken Creek in Fall 1999.

	Particle	Unit	N	Mean	s.e.
West Chicken Creek					
Forest	CPOM	riffle	5	48.0	21.9
		glide	2	38.9	30.9
		pool	3	189.1	102.6
	leaves	pool	1	6.8	
	FPOM	riffle	5	3.3	0.7
		glide	2	5.1	2.8
		pool	3	8.5	2.6
Transition	CPOM	riffle	5	23.8	15.0
		glide	4	52.0	29.6
		pool	1	14.2	
	leaves	riffle	2	10.4	8.9
	FPOM	riffle	5	5.2	1.4
		glide	4	3.3	0.1
		pool	1	3.1	
Meadow	CPOM	riffle	3	17.7	4.4
		glide	5	9.9	2.4
		pool	2	13.9	9.7
	FPOM	riffle	3	3.3	1.5
		glide	5	4.4	0.6
		pool	2	8.8	3.8

Appendix D2. CBOM storage (g/ m^2) in forest, transition, and meadow reaches of Limber Jim Creek in Fall 1999.

	Particle	Unit	N	Mean	s.e.
Limber Jim Creek					
Forest	CPOM	riffle	7	34.7	19.1
		pool	3	509.2	185.0
	leaves	riffle	3	5.0	2.2
		pool	3	6.9	5.7
	FPOM	riffle	7	1.3	0.3
		pool	3	16.9	8.9
Transition	CPOM	riffle	5	12.9	4.6
		glide	3	49.7	44.4
		pool	2	203.6	21.9
	leaves	riffle	1	1.9	
		pool	2	9.3	1.1
	FPOM	riffle	5	2.1	0.5
		glide	3	5.5	1.9
		pool	2	6.6	3.1
Meadow	CPOM	riffle	6	9.8	5.0
		glide	1	7.3	
		pool	3	148.7	98.9
	leaves	riffle	3	1.8	1.3
		pool	1	0.4	
	FPOM	riffle	6	1.6	0.4
		glide	1	2.4	
		pool	3	5.3	3.4